Breeding parameters of Great Cormorants (*Phalacrocorax carbo carbo*) at mixed species colonies on Prince Edward Island, Canada

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ABSTRACT

Breeding parameters of Great Cormorants (*Phalacrocorax carbo carbo*) and Double-crested Cormorants (*P. auritus auritus*) were examined at two mixed species colonies at Cape Tryon and Durell Point, Prince Edward Island from 1976 to 1978. Differential access to nests at the two colony sites resulted in more complete demographic data for *P. carbo* than for *P. auritus*.

In 1977, *P. carbo* was present at both colonies by 21 March, whereas *P. auritus* did not return until 1 April and 16 April at Cape Tryon and Durell Point, respectively. Differences in the arrival chronology by individuals of each species and differences in the time of nest site occupation according to age, are suggested as factors influencing the nest site distribution of *P. carbo* and *P. auritus* at Cape Tryon.

Forty-eight *P. carbo* chicks banded at the Durell Point colony between 1974 and 1976 returned there to nest as two- to four-year olds in 1977 and 1978. Unmarked individuals with clutch-starts in April were likely greater than four years old as all marked two to four-year olds (with one possible exception) in 1977 and 1978 had clutch-starts in May and June.

Seasonal variation in the breeding success of *P. carbo* individuals was examined at Durell Point in 1977. Mean clutch-size, hatching success and fledging success exhibited a seasonal decline. Four- and 5-egg clutches represented the majority (75%) of all *P. carbo* clutches at Durell Point in 1977 and had the highest reproductive success (0.48 and 0.43 chicks fledged per egg laid respectively). Smaller clutches produced small broods with significantly higher chick mortality while larger clutches suffered high egg loss prior to clutch completion.

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Dedicated to my parents

Mr. and Mrs. Alan H. Holman

Frontispiece. Great Cormorant

Phalacrocorax carbo carbo

INTRODUCTION

Cormorants (Phalacrocoracidae) are medium-sized to large aquatic birds specialized for fish-eating and are typically colonial-breeders, defending small nest territories vigorously. The Great Cormorant (*Phalacrocorax carbo carbo*) is the largest species (2600-4100 g, Appendix I), averaging 15 cm longer than the Double-crested Cormorant (*P. auritus auritus*) (Erskine 1972), which weighs approximately 1700-2600 g (Channing 1968). The two species are often confused in the field and occasionally in photographs (*e.g.*, Omand 1947; Canadian Wildlife Service 1973), although their identifying characteristics are quite distinct (*cf.* Godfrey 1966).

Phalacrocorax auritus is the most widely distributed Nearctic cormorant, breeding in both marine and freshwater habitats across Canada from southwestern Alaska to Mexico and the Bahamas (see map in Palmer 1962; Godfrey 1966). There are four subspecies with the nominate race, *P. a. auritus*, found in eastern Canada. *P. carbo* is the largest and most cosmopolitan cormorant in the world, breeding in marine and freshwater habitats from eastern Canada and Greenland through Europe, Africa, Asia, Australia and New Zealand (Fisher and Lockley 1954; Thomson 1964; see map in Cramp *et al.* 1977). There are eight subspecies with the nominate and largest race, *P. c. carbo*, found on the seacoasts of the North Atlantic (Godfrey 1966). It apparently extended its range to North America from Iceland and northern Europe following the last glaciation (Palmer 1962; Todd 1963). The species is widely dispersed with individuals reported to penetrate far inland through

mountain gorges in Asia (Cramp *et al.* 1977). Of four cormorant species whose dispersal was studied in south Australia, it was the only one to reach Tasmania (van Tets *et al.* 1976).

Phalacrocorax auritus is a migratory species. Most individuals from northeastern North America winter along the Florida coast (Kury and Cadbury 1970; Arbib 1974). The peak of the autumn migration passes through Cape Cod, Massachusetts in late September and October (Hill 1965), while the first birds return to the Gulf of St. Lawrence by late March or early April (Lewis 1929; photograph in Halifax Herald 6 April 1976). *P. carbo* is not truly migratory in North America (Lewis 1937; Todd 1963) as some individuals may remain in the vicinity of the breeding colonies throughout the winter if shallow water remains ice-free (Palmer 1962). Many winter from southern Nova Scotia along the New England coast (Kain 1974; Ross 1974; Duffy and LaFarge n.d.). However, first-year birds may travel farther. For example, one immature was observed on Lake Ontario near Toronto 14 January 1978 (Goodwin 1978) and a nestling banded at Durell Point, Prince Edward Island 16 June 1974 was shot in South Carolina later that fall. Recent reports of *P. carbo* wintering farther south to South Carolina and Florida are increasing (Desante 1976; Howe 1978) and in 1977 they were first observed in Louisiana (Hamilton 1978).

Phalacrocorax carbo and *P. auritus* are highly adaptable in their breeding requirements and have many pronounced similarities (Ross 1973). Both species are in the same category of nesting and feeding requirements (van Tets 1959), but in different groups according to size and plumage characteristics (van Tets 1974). In Europe, where *P. carbo* and the strictly marine Shag, *P. aristotelis*, are sympatric, *P. carbo* occupies both

marine and freshwater habitats (Witherby *et al.* 1965; West *et al.* 1975; D. Cabot pers. comm.). However, in North America *P. carbo* is confined to marine environments (Palmer 1962; Ross 1973), rarely straying from coastal areas (see map in Palmer 1962; Tufts 1973). Colonies are located on rocky islets or cliffs, generally on the more elevated positions (Bayley 1925; Palmer 1962). *P. auritus* also nests in these locations (Palmer 1962; Hubbs *et al.* 1970; Drury 1974). In addition, *P. auritus* frequently nests in trees (Godfrey 1966; Reed 1973) and occasionally in atypical situations including high power poles (Stallcup and Winter 1976), abandoned wharves (Jewett *et al.* 1953; Tufts 1973), shipwrecks (G. Chapdelaine, pers. comm.) and on floating mats of dead vegetation (Anderson and Hammerstrom 1965). Although *P. carbo* frequently nests in trees elsewhere (West *et al.* 1975, Cramp *et al.* 1977), it rarely does so in North America (Godfrey 1966).

Very little detailed information on the reproductive demography of *P. c. carbo* has been published. Cramp *et al.* (1977, p. 206), who provided the most comprehensive documentation of the species' biology to date, followed the heading 'breeding success' with "no data". There have been no detailed studies on clutch-size. The average clutch-size for *P. carbo* has been recorded at three to four eggs (Witherby *et al.* 1965; Lock and Ross 1973) or four to five and occasionally six eggs (Bent 1922; Tufts 1973). Erskine (1972) relied on data in the Maritime Nest Records Scheme to suggest that the highest values were unrepresentative and that the most frequent clutch-size was three eggs.

The breeding biology of *P. auritus* has been well studied (Lewis 1929; Mendall 1936) and there have been numerous studies on other aspects of the biology of the species (*e.g.*, Taverner 1915; Drewien and Fredrickson 1969;

De La Ronde and Greichus 1972; Dunn 1975a, 1975b). Vermeer (1970) briefly described the spring arrival and clutch-initiation of *P. auritus* at an Alberta colony. van Tets (1959) conducted a comparative study of the reproductive and natural history of *P. auritus* and two other cormorant species (Pelagic Cormorant, *P. pelagicus*, and Brandt's Cormorant, *P. penicillatus*) in British Columbia.

The most thoroughly studied cormorant species to date is *P. aristotelis*. Lack (1945) showed that *P. aristotelis* and *P. carbo* in Britain differ widely in their feeding and nesting requirements and concluded that their distribution was a good example of Gause's hypothesis (1934) that two species with similar ecology cannot live in the same area. However, Coulson (1961) concluded that the use of these two species to support Gause's hypothesis was not as convincing as has been claimed. Finally, Snow (1960, 1963) studied the behaviour and seasonal aspects of the breeding biology of *P. aristotelis* while Potts (1966) concentrated on the breeding biology of known-age birds.

Studies of known-age birds allow for the investigation of particular age-related aspects of their biology that are generally unavailable in most other studies. Unfortunately, few such seabird studies exist (*e.g.*, Richdale 1951, 1957; Austin and Austin 1956; Coulson and White 1958, 1960; Potts 1966). These and similar studies on other avian groups (*e.g.*, Nice 1937; Kluijver 1951; Perrins 1965) have generally shown that variations in various reproductive parameters of the breeding cycle stabilize with age or breeding experience of individuals and that this stability is associated with increased breeding efficiency (Potts 1966).

A major problem often encountered in colonial seabird studies is the "observer effect". The negative effect of human disturbance on cormorant colonies has been well documented (Berry 1974; Norman 1974; Kury and Gochfeld 1975; Ellison and Cleary 1978). Predators (gulls and crows) often take unprotected eggs and small chicks when adults abandon their nests at the approach of investigators (Gross 1944; Drent *et al.* 1964). *P. carbo* are often very bold at their nests, particularly when chicks are present (Lewis 1931; Todd 1963).

The North American range of *P. carbo* is bounded on all sides by that of *P. auritus* (Erskine 1972). However, very little is known about the ecology of the two species where they are sympatric. Ross (1973) examined the foods taken by each species and briefly described their nesting habitat at mixed species colonies on small rocky islands in Nova Scotia. A list of the known mixed species colonies of *P. carbo* and *P. auritus* is in Appendix II. Prince Edward Island, situated in the southwestern Gulf of St. Lawrence, is within the sympatric breeding range of these species. In contrast to Nova Scotia, where most colonies are on small offshore islands (Ross 1973), all Prince Edward Island colonies are located on mainland sandstone cliffs. The known histories of the six cormorant colonies on Prince Edward Island are in Appendices III, IV and V. Both the Cape Tryon and Durell Point colonies have a history of persecution (shooting by vandals) prior to the late 1960's or early 1970's (local residents, pers. comm.). *P. carbo* was first recorded to be nesting at Durell Point in 1952 at a time when 15 nests were on the cliff and four in low stunted spruce trees (Godfrey 1954; Appendix III). *P. auritus* did not occupy this colony until 1975 (pers. obs.). The first report of cormorants nesting at Cape Tryon was in 1936 (Peters in Erskine 1972).

Since then, both species have occupied the colony continuously (Appendix IV), making it the oldest known mixed *P. carbo/P. auritus* colony in North America. The cliff-shelves (sloping area above cliff-face) and base at Cape Tryon have been utilized as nesting habitat by the cormorants more recently than the cliff-face. In 1960 the only cormorant nests observed were on the cliff-face (G. F. van Tets' photographs and unpublished field notes). No cormorants occupied the shelves, and the base was used only as a roosting area by both species. With colony expansion, cormorants that nested on the cliff-shelves were more susceptible to predation and human disturbance than those on the cliff-face and nests at the base were more susceptible to destruction by heavy seas.

My major objectives in the present study were primarily directed at elucidating breeding parameters of the *P. carbo* colony at Durell Point by focussing on:

1. clutch initiation according to age of breeding individuals, and
2. comparison of the relative proportion and success of different-sized clutches.

In addition, factors that influence the nesting distribution of *P. carbo* and *P. auritus* were to be examined at Cape Tryon. While the information collected on the latter is likely incomplete, it is hoped that a more thorough study on this aspect of their ecology may be stimulated by the following account.

Methods

1. Study Areas

The principal study areas were mixed colonies of both cormorant species at Durell Point and Cape Tryon on the east and north shores of Prince Edward Island respectively (Fig. 1). The locations of other colonies on Prince Edward Island are also shown in Figure 1. The geographic relationship of the study areas relative to other cormorant colonies in Atlantic Canada is shown in Figure 2.

The *P. carbo* colony at Durell Point was located on a sandstone cliff ranging in height from 12 to 27 m on the wooded north side of a headland surrounded by shallow bays (Fig. 3). The lower portion of the cliff was a perpendicular rock face with few ledges while the upper portion was an unstable, earth-covered slope of varying steepness, strewn with protruding rocks and fallen trees. The trees above the cliff were mainly *Picea glauca* and *Abies balsamea*. The entire colony extended approximately 300 m along the cliff-face and was comprised of four major, but loosely joined, nesting concentrations.

The cormorant colony at Cape Tryon was located on a vertical, sandstone cliff that rose approximately 33 m from shallow water (Fig. 4). Numerous cliff-face ledges provided nest sites for both cormorant species. In addition, the sloping area above the cliff-face (shelves) and rocky base and talus slope at the west end of the colony were also available as nesting habitat. However, trees were absent above the colony (Fig. 4). The colony was restricted to a stretch of cliff approximately 500 m long as on either side, the cliff decreased in height and lacked suitable nesting sites. Because the entire colony was visible

Figure 1. Location of cormorant colonies on Prince Edward Island between 1973 and 1978 (Brown *et al.* 1975; pers. obs.).

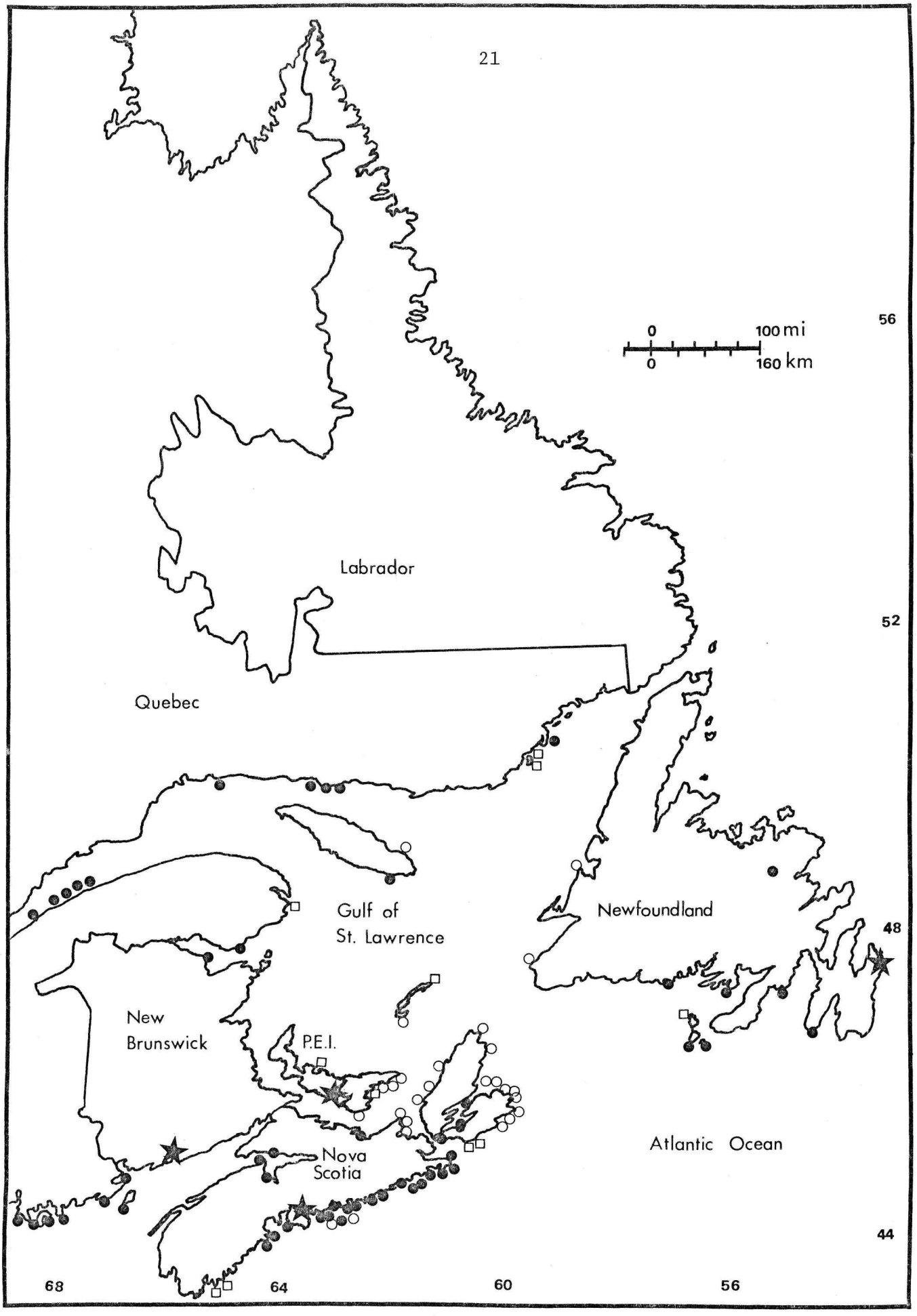

0 100 mi
0 160 km
Labrador
Quebec
Gulf of
St. Lawrence
Newfoundland
New
Brunswick
P.E.I.
Nova
Scotia
Atlantic Ocean
56
52
48
44
68
64
60
56

Figure 2. Location of known cormorant colonies in the Gulf of St. Lawrence and surrounding areas between 1971 and 1978 (Lock and Ross 1973; Ross 1973; Brown *et al.* 1975; G. Chapdelaine pers. comm.; pers. obs.). Open and closed circles represent *P. carbo* and *P. auritus* respectively while open squares represent mixed *P. carbo*/*P. auritus* colonies. The locations of major cities are indicated by stars.

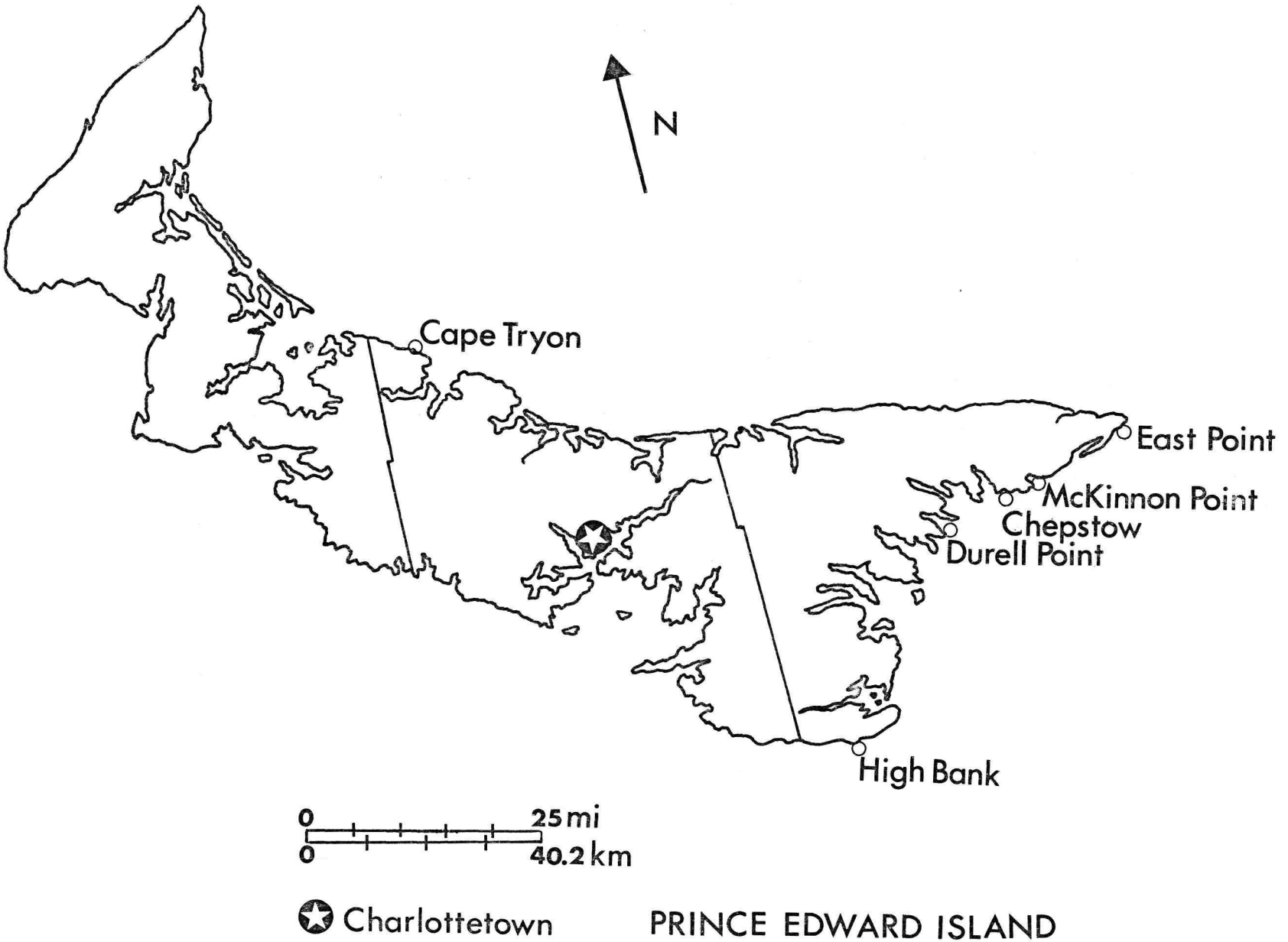

N
Cape Tryon
East Point
McKinnon Point
Chepstow
Durell Point
High Bank
0
25 mi
0
40.2 km
Charlottetown
PRINCE EDWARD ISLAND

Figure 3. Cormorant colony at Durell Point, Prince Edward Island in 1976.

Figure 4. Cormorant colony at Cape Tryon, Prince Edward Island in 1976.

only from the water, detailed observations were conducted only on those cormorants that nested along the western half and at the extreme eastern end of the colony.

2. Observational Techniques

During much of the 1976 field season and for part of the 1977 season, data on nesting distribution and overall reproductive success of both *P. carbo* and *P. auritus* were collected at each of the two main colonies by using a spotting scope (20x and 40x power lenses) and binoculars. A blind was unnecessary and the observer generally sat approximately 10 m from the closest nests. In 1976, the entire colony at Durell Point (except for three nests) was observed from one location. Observations at Cape Tryon were conducted from two locations throughout the study, one at either end of the colony.

Visitation rates in 1976 were every other day at each colony from 23 April to 11 September with observation periods lasting one to four h per day depending upon the time of the breeding season and the number of birds using the colony. In 1977 the field season commenced 21 March prior to the arrival of *P. auritus* at a time when less than half the eventual number of *P. carbo* individuals were present at the colonies. Observation periods lasted one to eight h. Both colonies were visited daily in 1977 until 24 April when most birds had returned. Thereafter, daily visits to Durell Point continued until 1 September, but visits to Cape Tryon were reduced to every other day until 12 May and to once per week until 1 September.

The major emphasis of the 1977 season was collection of intensive demographic data on *P. carbo* at Durell Point made possible by daily nest checks. Daily nest checks were not possible at Cape Tryon and reproductive success was assessed by the number of chicks fledged per nest. Information on arrival chronology and nest site choice by both species was collected in 1977 primarily during the early part of the season until 24 April at Cape Tryon.

3. Demographic Data

The 1977 field season (21 March to 1 September) was spent primarily collecting demographic data on *P. carbo* at Durell Point, where all but three nests were accessible. With the appearance of the first egg each nest was identified by a numbered stake driven into the ground beside the nest. Thereafter, all nests were checked daily and the fates of their contents recorded. The length and width (mm) of all eggs were measured (Appendix VI) and eggs were numbered according to their sequence in the clutch. The complete hatching sequence was determined where possible (n = 81, 60.8%) and, upon hatching, chicks were marked with numbered web tags. At two weeks of age or older chicks were banded with U. S. Fish and Wildlife Service bands and the web tags were removed. Chicks from 4-egg (n = 17) and 5-egg (n = 21) clutches were weighed every other day from hatching until they reached a weight of 2000 g. Chicks of this weight (three weeks or older) became increasingly mobile such that close approach by the investigator greatly increased their risk of falling off the cliff. Accordingly, from early July to the end of the 1977 field season, nests were observed daily from outside the nesting area to record the number of chicks fledging per nest.

4. Banding and Colour-Banding

Between the years 1974 and 1978, 583 *P. carbo* nestlings were banded at Durell Point. In addition to the annual banding of *P. carbo* nestlings, 51 adult *P. carbo* were also banded at Durell Point. Adults were captured at their nests during 1976 and 1977 by using a modification of the noosing technique used by Edgar (1968) for the Australian Gannet (*Sula serrator*). Each adult was banded with a numbered aluminum band and one or more coloured plastic bands. Thirty-one of these birds were weighed (g) and bill measurements (length, depth mm) were taken (Appendix I). As a consequence of this four year banding program, there were two known-age classes of *P. carbo* at Durell Point by 1976. In 1978 there were five known-age classes following the banding of early-nesting adults in 1977 which were assumed to be more than three years old (see below). Thus, the 1978 field season (27 May to 14 June) was devoted to the collection of data on breeding *P. carbo* of known-age at Durell Point.

5. Experimental Nest Sites

The number of suitable nesting sites on the cliff at Durell Point was limited to places where a support was provided by boulders or fallen trees or to areas of level terrain (pers. obs.). I created additional nesting sites on the cliff in 1977 to test the hypothesis that *P. auritus* nests in the trees at Durell Point and not on the cliff because of a lack of sites due to earlier occupancy by *P. carbo*. Accordingly, 37 concrete blocks (40 x 20 x 30 cm) and eight logs were secured on the cliff in the central colony location below trees occupied previously by *P. auritus*. Twenty-seven blocks were placed on the cliff 20-26 February 1977 when approximately

50 *P. carbo* were occupying the colony, while the remaining 10 blocks were positioned on 16 May amidst occupied *P. carbo* nests.

RESULTS

I. Colony Tenacity and Pre-nesting Behaviour

At least 4-5% of all *P. carbo* nestlings banded at Durell Point from 1974 to 1976 returned there to breed as two-year olds between 1976 and 1978. Further, there was a trend toward increased breeding with age (Table 1). Band recoveries from all *P. carbo* nestlings banded at Durell Point are tabulated in Appendix VII. Of 74 chicks banded in 1974, at least 13 (17.6%) were found breeding at the Durell Point colony between 1976 and 1978. Of these, only three bred as two-year olds, whereas 11 and 10 individuals bred as three-year olds and four-year olds respectively (Table 1).

Individuals colour-banded as breeding adults also exhibited colony tenacity. At least 33 (67.4%) breeding adults captured in 1976-1977 returned to the colony the following year. Two colour-banded *P. carbo* were observed at the McKinnon Point colony (Fig. 1), one at a nest with four chicks. Three banded *P. carbo* were seen at the Chepstow colony (Fig. 1). One bird was occupying a nest. No banded adult *P. carbo* were observed at Cape Tryon, although on several occasions a banded immature *P. carbo* was roosting there. No other *P. carbo* colour-banding schemes exist in North America.

Prior to pair formation, males of both species performed a mate-advertising display ("wing-waving", see van Tets 1965) at the chosen nest site. During this display, *P. carbo* males remained silent, whereas male *P. auritus* vocalized. The females of each species responded only to the correct males and no interspecific copulatory attempts were observed.

Table 1. Number of known-age *P. carbo* breeding at Durell Point between 1976 and 1978. Percentage of each age class is in parentheses.

Hatching year	Number banded (n)	Year		
		1976	1977	1978
1974	74	3 (4.05)	11 (14.87)	10 (13.51)
1975	100	--	5 (5.00)	7 (7.00)
1976	147	--	--	7 (4.76)

"Wing-waving" ceased following mate selection, even when the first nesting attempt failed and the pair continued to occupy the site. Males whose original mate abandoned the site following a nesting failure re-initiated the "wing-waving" behaviour to attract another mate. This has also been described for *P. aristotelis* (Snow 1963), and was used here as evidence that the same two birds renested.

II. Utilization of Nesting Habitat

Cormorants at the Cape Tryon colony occupied three major nesting habitats during the three years of this study. Sixty-three to 68 (42.0-43.0%) *P. carbo* pairs nested annually on the cliff-face ledges and 87-90 (57.0-58.0%) pairs nested on the sloping shelves above the cliff-face (Table 2). Three hundred and two to 339 (81.6-85.1%) *P. auritus* pairs nested annually on the cliff-face ledges and 50-64 (13.6-17.0%) pairs nested among the fallen debris at the cliff-base. In 1976 and 1977, three to five (0.81-1.35%) *P. auritus* pairs also built nests among *P. carbo* nests on the cliff-shelves (Table 2). The 1976 nest site distribution of *P. carbo* and *P. auritus* at the western portion of the colony, as viewed from the water, is in Figure 5. Other species that nested on the cliff at Cape Tryon from 1976 to 1978 included Bank Swallows (*Riparia riparia*), Common Starlings (*Sturnus vulgaris*) and Rock Doves (*Columba livia*).

Phalacrocorax carbo and *P. auritus* individuals both occupied broad ledges on the cliff-face. However, *P. auritus* also utilized smaller ledges. For example, in 1976 a *P. carbo* pair unsuccessfully attempted to construct a nest on a small ledge on the cliff-face that was occupied successfully by a *P. auritus* pair in 1975, 1977 and 1978 (Fig. 6). At

Table 2. Number of *P. carbo* and *P. auritus* pairs nesting on the three major nesting habitats at Cape Tryon from 1976 to 1978. Percent of total is in parentheses.

Habitat	Year					
	1976		1977		1978	
	P. carbo	*P. auritus*	*P. carbo*	*P. auritus*	*P. carbo*	*P. auritus*
cliff shelves	90 (57.3)	5 (1.35)	90 (57.0)	3 (0.81)	87 (58.0)	0
cliff face	67 (42.7)	302 (81.6)	68 (43.0)	314 (85.1)	63 (42.0)	339 (84.1)
cliff base	0	63 (17.0)	0	50 (13.6)	0	64 (15.9)
Total	157	370	158	369	150	403

Figure 5. Distribution of cormorant nests at the west end of the Cape Tryon colony in 1976. Circles represent breeding pairs and squares represent non-breeding pairs. Drawn from photographs and direct observation of the study area.

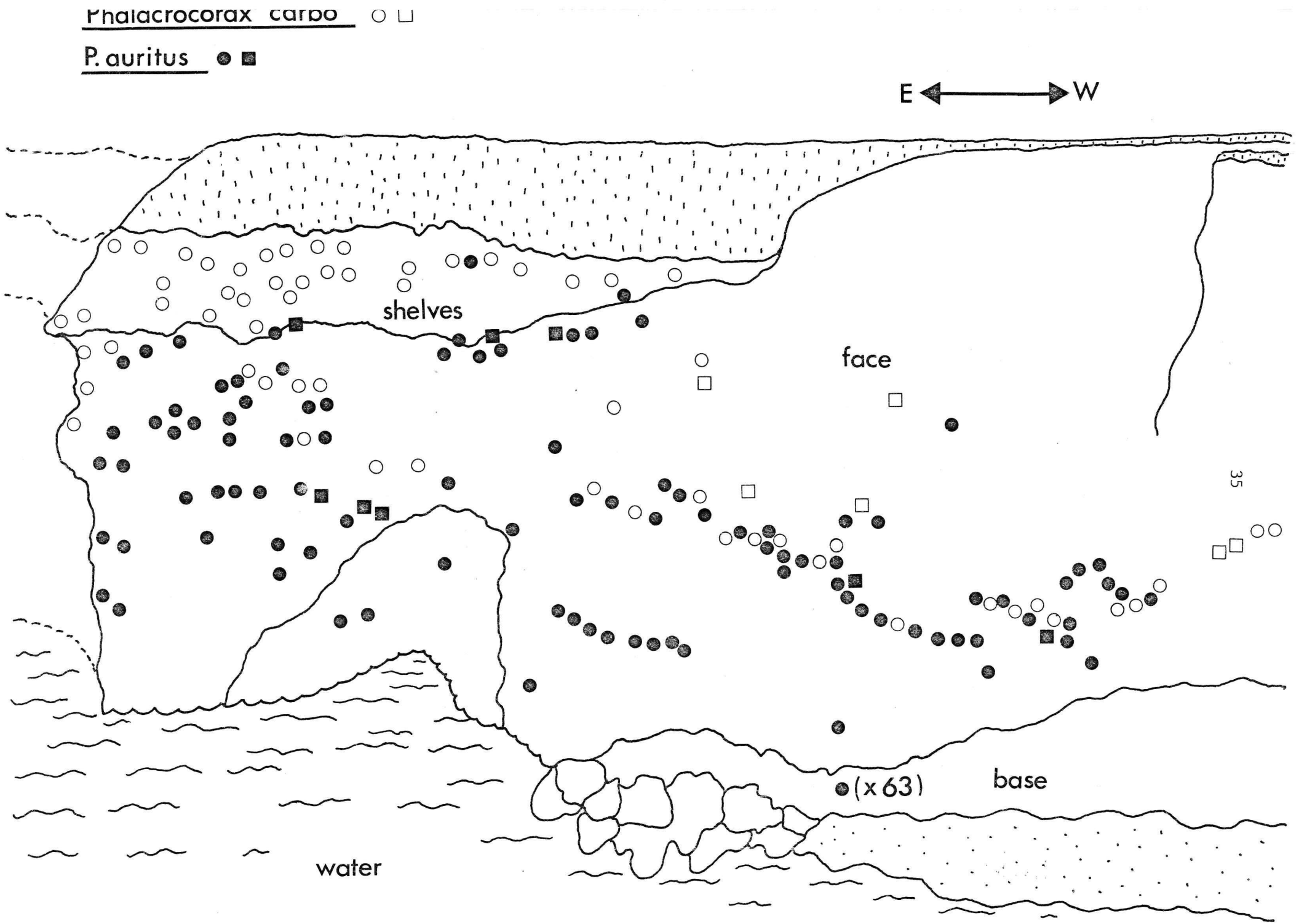
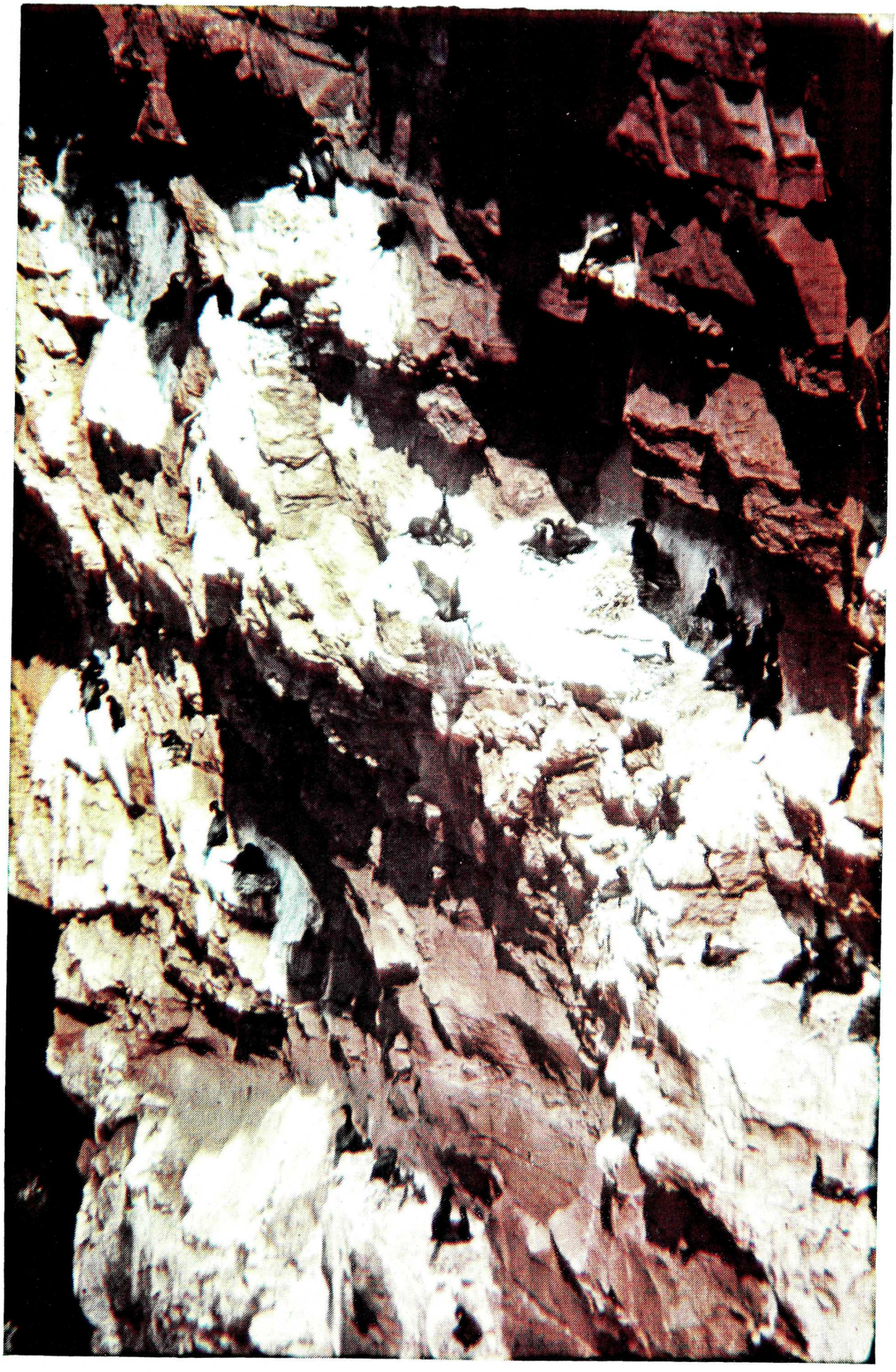

Phalacrocorax carbo ○ □
P. auritus ● ■
E
W
shelves
face
35
(x 63)
base
water

Figure 6. *P. carbo* and *P. auritus* cliff-face nest sites at Cape Tryon in 1976. The arrow indicates a ledge suitable as a nest site for *P. auritus* but not for *P. carbo*.



least 14 (10.8%) nest sites in 1977 and 12 (9.8%) in 1978 were exchanged between the two species from the previous year (Table 3).

At Durell Point, 153-183 (97.5-98.4%) *P. carbo* pairs annually occupied the sloping area above the cliff-face and three to four (1.6-2.5%) pairs occupied three ledges on the cliff-face during the three years of this study. With the exception of one pair in 1976, no *P. carbo* nested in trees at this colony, although occasionally a pair constructed a nest on a fallen tree on the cliff. Fifty-nine (95.2%) *P. auritus* pairs nested in trees on or above the cliff between 1975 and 1978, and only three (4.8%) pairs constructed nests supported against the bases of trees on the cliff. Other birds nesting at this colony throughout the study included several pairs of Black Guillemots (*Cepphus grylle*), one to two pairs of Great Black-backed Gulls (*Larus marinus*), one pair of Common Ravens (*Corvus corax*), and numerous Common Starlings.

In 1977 at Durell Point seven (4.6%) *P. carbo* pairs constructed nests on the concrete blocks placed on the cliff and on numerous occasions single male *P. carbo* were observed "wing-waving" on other blocks. One *P. auritus* pair occupied a block on 3 June 1977, however, no *P. auritus* nested there despite the availability of 25 unoccupied blocks upon the arrival of the first *P. auritus*.

III. Chronology of Arrival

Phalacrocorax carbo pairs were observed on 20 February 1977 occupying old nest sites at Durell Point. However, it was not known if these individuals remained together until the breeding season. No adult *P. carbo* were at Cape Tryon on 19 February 1977, although two immature birds were

Table 3. Number of cliff-face nest sites exchanged between *P. carbo* and *P. auritus* at Cape Tryon from 1976-1977 and from 1977-1978. Only those pairs nesting at the west end of the colony are considered. The percentage of cliff-face nest sites that were exchanged is in parentheses.

first species ⟶ second species	Pairs changing nest sites (n)	
	1976-1977	1977-1978
P. carbo ⟶ *P. auritus*	4 (14.3)	4 (12.9)
P. auritus ⟶ *P. carbo*	10 (9.8)	8 (8.7)
Total	14 (10.8)	12 (9.8)

seen in the vicinity. On 24 February 1977, a flock of 20 cormorants was observed five km west of Cape Tryon at Sea View (N. Hurry, pers. comm.).

Little specific information was collected on the chronology of arrival of *P. carbo* at Durell Point in 1977, but in general it resembled that at Cape Tryon (see below). *P. auritus* arrived at Durell Point on 16 April 1977, more than two weeks later than at Cape Tryon. The first *P. auritus* pairs occupied old nest sites 22 April and by 6 May six (54.6%) of the pairs that eventually nested there occupied nest sites.

The chronology of arrival of *P. carbo* and *P. auritus* pairs at nest sites at Cape Tryon in 1977 is summarized in Table 4. By 22 March, 7 *P. carbo* pairs occupied nest sites on the cliff-face at the west end of the colony. Nest sites on the cliff-shelves were not occupied until 1 April 1977, when 13 of the 31 (41.9%) cliff-face sites eventually occupied by *P. carbo* at the west end of the colony were already "claimed" by pairs and a further 10 (32.3%) nest sites were "claimed" by single males. The chronology of nest site occupation on the cliff-face and shelves by *P. carbo* pairs is in Figure 7. The peak of new occupants on the cliff-face occurred from 5 to 10 April. However, the number of new occupants continued to increase on the shelves and reached a peak from 5 to 10 May. A period of inclement weather (11-15 April 1977) resulted in a lull in nesting activity.

Phalacrocorax auritus individuals were first observed in the vicinity of Cape Tryon 1 April 1977, and the first pairs occupied nest sites on 7 April (Table 4). The chronology of nest site occupation by *P. auritus* and *P. carbo* is in Figure 8. The early peak of nesting by *P. auritus* (25-30 April) represents occupancy of the cliff-face while the late peak (25-31 May) represents occupancy of the cliff-base. *P. auritus* arrived at

Table 4. The chronology of arrival of *P. carbo* and *P. auritus* pairs at nest sites at Cape Tryon in 1977. The percentage of the eventual total occupants for each nesting habitat is in parentheses.

Approximate percentage of total occupants	Species			
	P. carbo		*P. auritus*	
	cliff-face n = 31	cliff-shelves n = 28	cliff-face n = 92	cliff-base n = 50
first occupancy	<22 March	1 April	7 April	23 April
25%	22 March (0.32)	17 April (0.29)	22 April (0.38)	9 May (0.34)
50%	7 April (0.55)	28 April (0.57)	26 April (0.53)	16-19 May (0.50)
75%	22 April (0.74)	4 May (0.71)	6 May (0.75)	24-31 May (0.88)
95%	12-16 May (0.94)	6-9 May (0.96)	24-31 May (0.99)	31 May-9 June (1.00)

Figure 7. Date of nest site occupation by *P. carbo* pairs on the cliff-face and shelves at Cape Tryon in 1977; 7 pairs occupied nest sites on the cliff-face prior to the beginning of the 1977 field season. The number of new pairs is shown for each 5-day block.

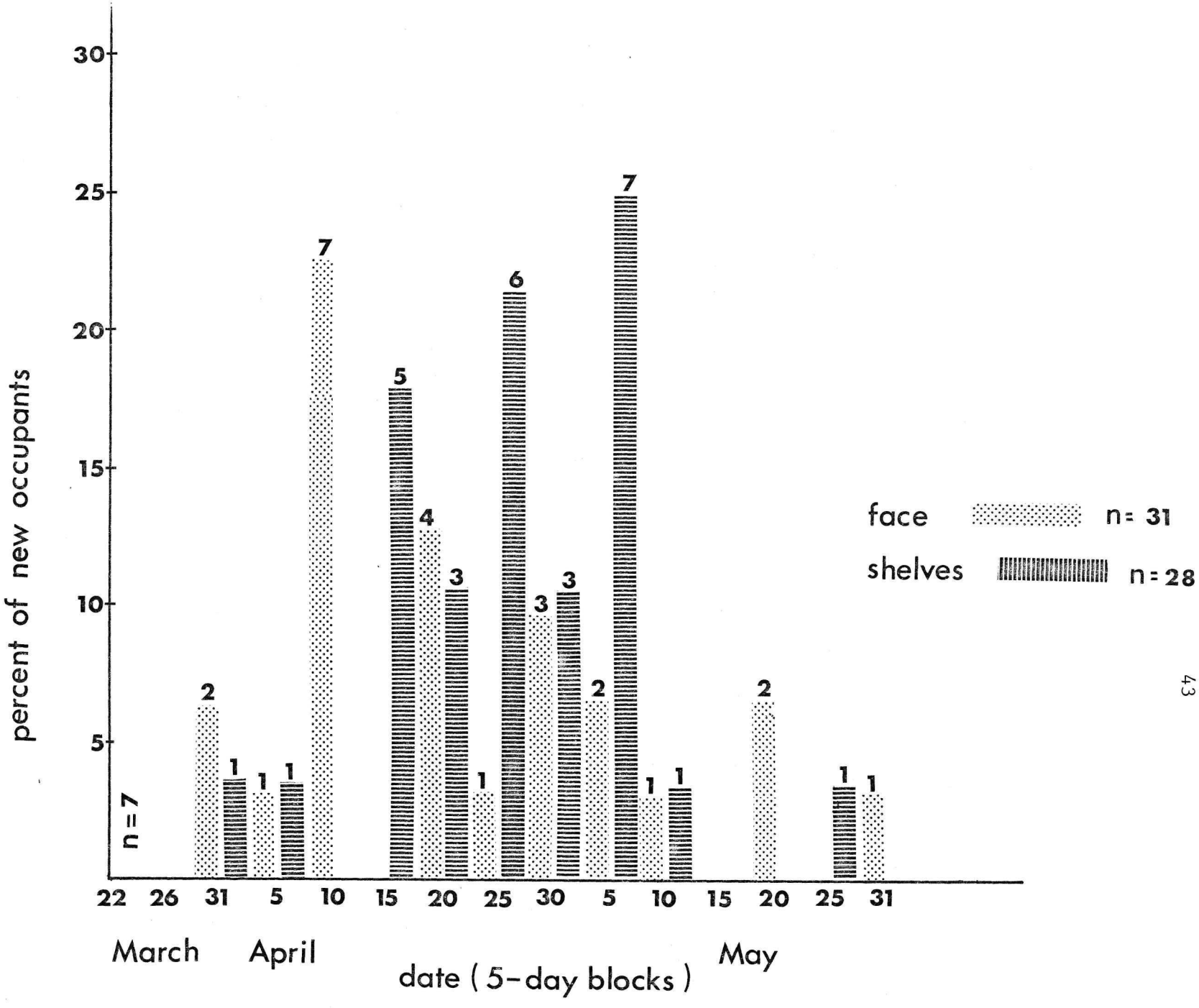
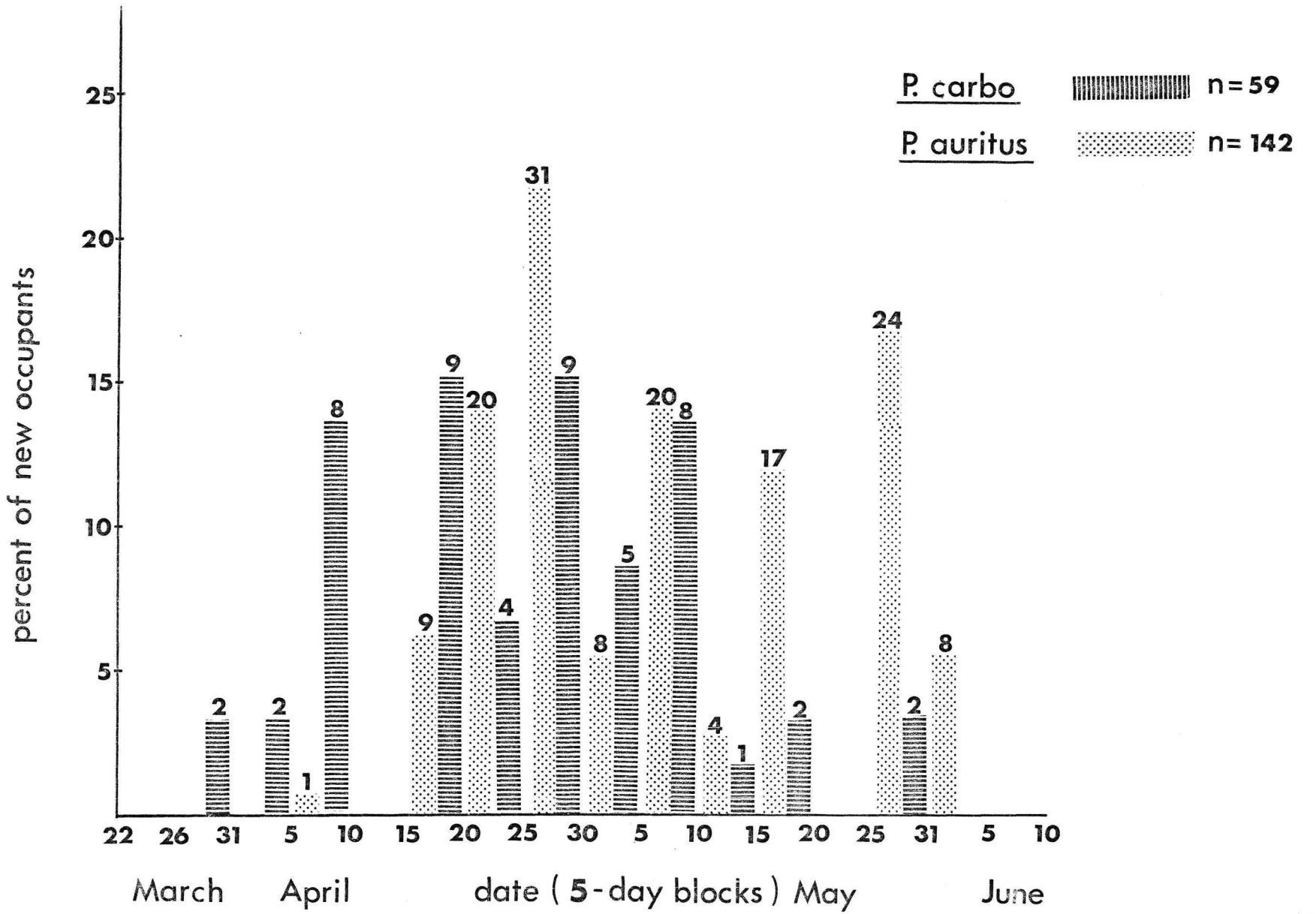

30
25
20
15
10
5
percent of new occupants
n=7
2
1
1
1
7
5
4
3
1
6
3
3
2
7
1
1
2
1
1
face
n= 31
shelves
n= 28
22
26
31
5
10
15
20
25
30
5
10
15
20
25
31
March
April
May
date (5-day blocks)

Figure 8. Date of nest site occupation by *P. carbo* and *P. auritus* pairs at Cape Tryon in 1977. The number of new pairs is shown for each 5-day block.

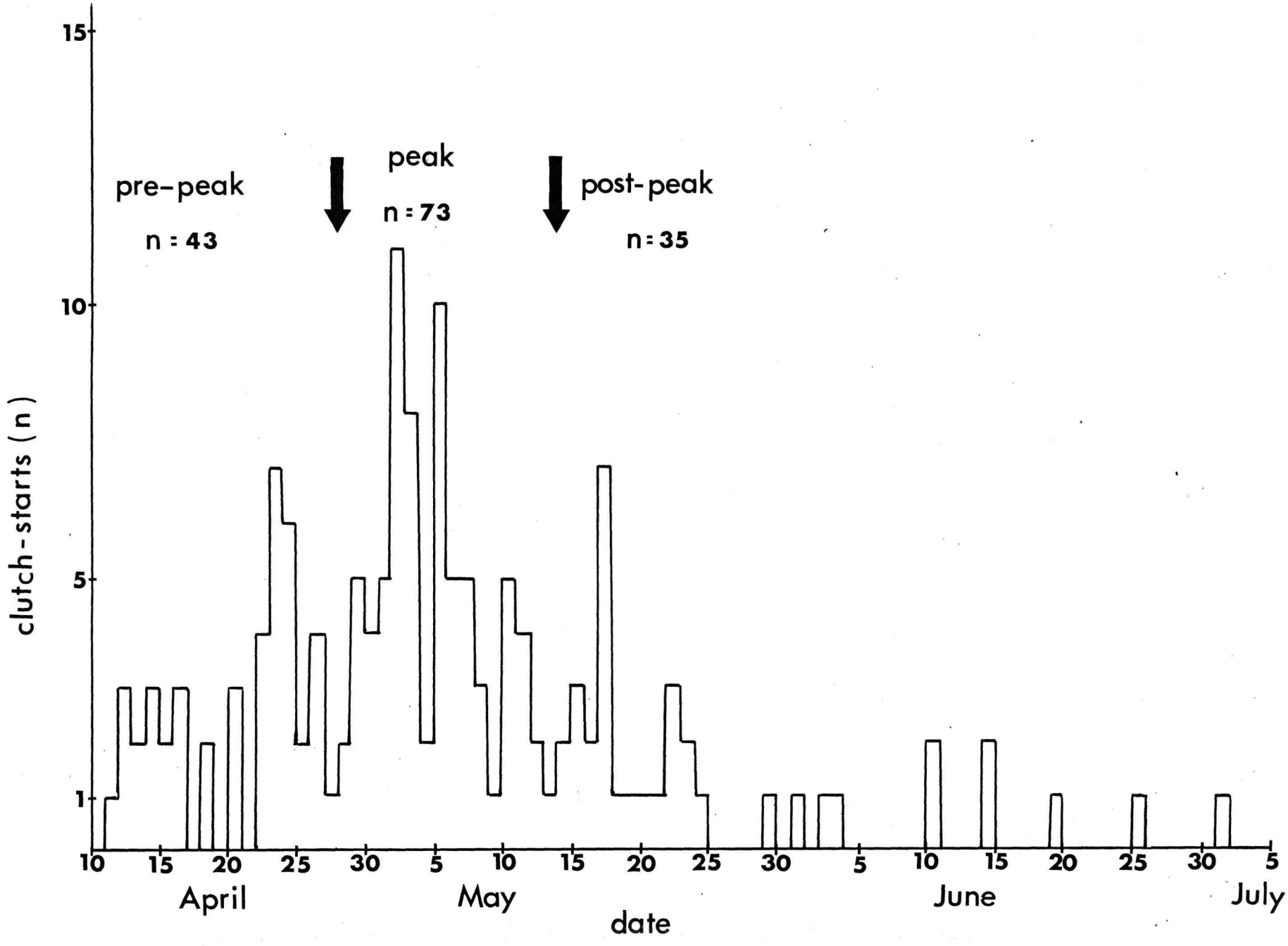

P. carbo
n = 59
P. auritus
n = 142
percent of new occupants
25
20
15
10
5
2
2
1
8
9
9
20
4
31
9
8
5
20
8
4
1
17
2
24
2
8
22
26
31
5
10
15
20
25
30
5
10
15
20
25
31
5
10
March
April
date (5 - day blocks) May
June

Cape Tryon three days following the first observation of "wing-waving" *P. carbo* males on the cliff-shelves. At this time there were still six vacant nest-sites on the cliff-face that were eventually occupied by *P. carbo*. The peak period (25-30 April) for establishment of nest sites on the cliff-face by *P. auritus* pairs occurred when most new *P. carbo* pairs were establishing sites on the cliff-shelves (Fig. 7).

IV. Chronology of clutch-start by *P. carbo*

Three major peaks of clutch-start (defined here as laying of the first egg of the clutch) activity by *P. carbo* were observed at the Durell Point colony during the 1977 breeding season (Fig. 9). The initial peak (24 April) occurred 13 days following the first clutch-start. The middle (3 May) and final (18 May) peaks occurred 22 and 37 days following the first clutch-start respectively. In order to examine changes in reproductive success with time of clutch-start, the breeding season was segregated into three periods based around these three peaks. The early (pre-peak) period included all clutches initiated between 12 and 27 April. The middle (peak) and late (post-peak) periods included all clutches initiated between 28 April and 14 May,and 15 May and 2 July respectively. Replacement clutches were not included. The split dates chosen may be considered arbitrary, although they represent the three most prominent peaks of clutch-start activity during the breeding season. Additional analysis of the data by separating the clutch-starts into a 50/50 split, similar-sized early, middle and late samples, and into 9-day intervals yielded a distribution of demographic data similar to that acquired with the split dates noted above (Appendix VIII).

Figure 9. Chronology of clutch-start by *P. carbo* at Durell Point in 1977.


15
10
5
1
clutch-starts (n)
pre-peak
n = 43
peak
n = 73
post-peak
n = 35
10
15
20
25
30
5
10
15
20
25
30
5
10
15
20
25
30
5
April
May
June
July
date

Most (n = 145) *P. carbo* clutches in 1978 were initiated prior to my arrival on 27 May. Accordingly, the estimated dates of clutch-start were determined to within five days by backdating from the age of the largest chick (Fig. 10). Chick age was estimated by comparison with weight and/or stage of development of known-age chicks.

A combined total of 48 marked two-, three- and four-year old *P. carbo* nested at Durell Point in 1977 and 1978. Twenty marked two- and three-year olds nested during the 1977 peak and post-peak periods (Table 5) yet none nested during the pre-peak period. Eight of the 11 marked three-year olds nested during the 1977 peak period compared to only one of the five marked two-year olds (Table 6). The difference between the clutch-start times of these two age classes approached significance (Fisher Exact Probability Test, Siegel 1956, $p = 0.077$). With the exception of one individual (a two-year old male), all marked two-, three- and four-year old *P. carbo* in 1978 had clutch-starts later than 1-5 May (Table 6). In contrast, 13 *P. carbo* captured as breeding adults in 1977 had clutch-starts in 1978 prior to 1-5 May (Table 6). Nine of these individuals had clutch-starts during the pre-peak period in 1977. Only two (13.3%) of the adults captured in 1977 had clutch-starts in 1978 later than 1-5 May.

V. Chronology of Egg-laying by *P. carbo*

Clutch-size is defined here as the total number of eggs laid by one female for a single nesting (van Tyne and Berger 1961). The clutch-size distribution for *P. carbo* at Durell Point in 1977 is in Table 7. Replacement and incomplete clutches in nests lost during the egg-laying period are not included. Clutch-size ranged from one to eight eggs

Figure 10. Estimated chronology of clutch-start by *P. carbo* at Durell Point in 1978. The dashed line represents 40 clutches whose clutch-start dates could not be determined as no eggs were laid or hatched in these nests between 27 May and 14 June.

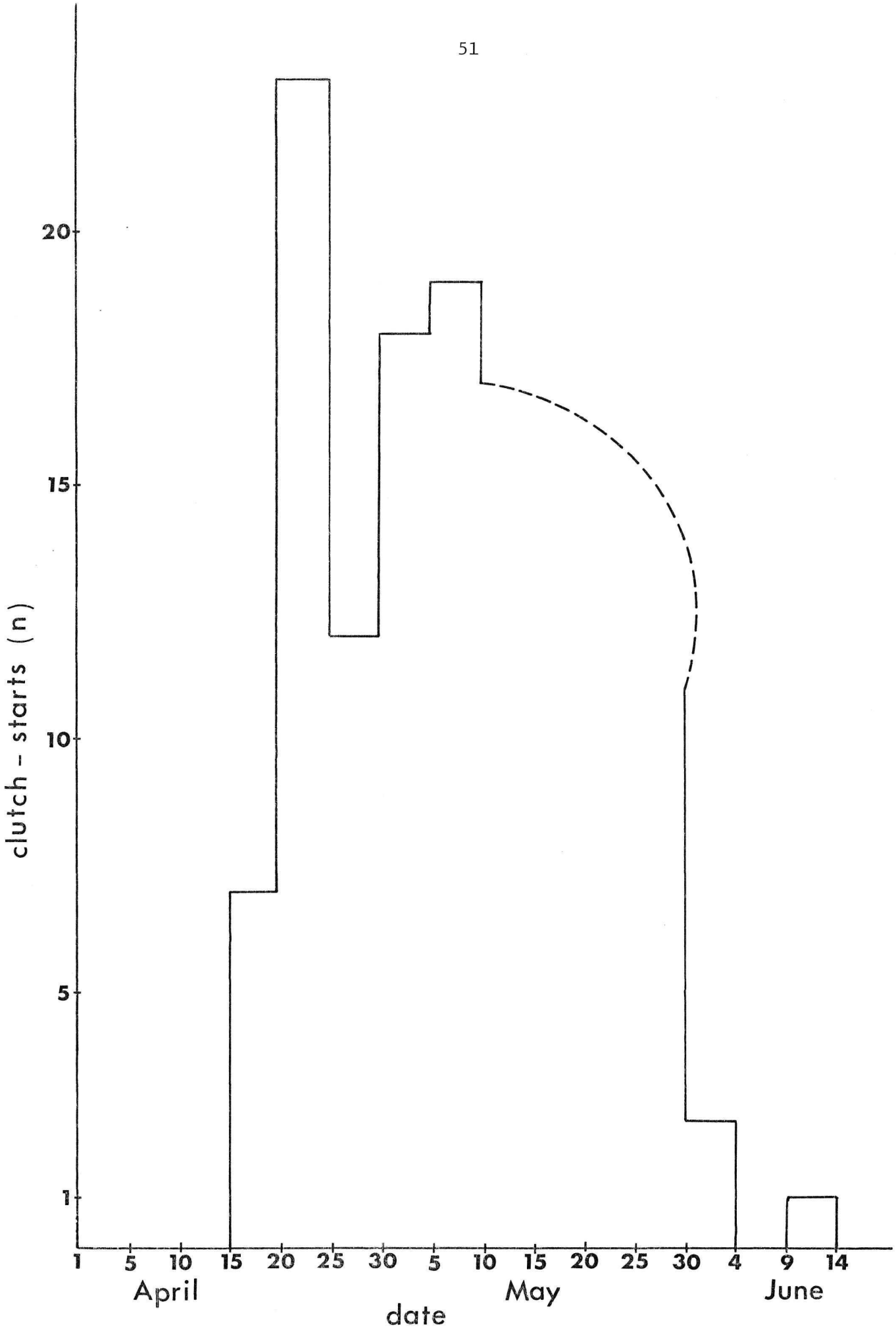

clutch - starts (n)
20
15
10
5
1
1
5
10
15
20
25
30
5
10
15
20
25
30
4
9
14
April
May
June
date

Table 5. Number of known-age *P. carbo* nesting at Durell Point in 1977. The percentage of each age class and the sex ratio (when known) are in parentheses.

Dates	Age		
	2 year	3 year	2 or 3 year
12-27 April (pre-peak)	0	0	0
28 April-14 May (peak)	1 (0.20, 1♂)	8 (0.73, 6♂, 2♀)	1 (0.25)
15 May-2 July (post-peak)	4 (0.80, 2♂, 2♀)	3 (0.27, 3♂)	3 (0.75, 1♂ 2?)
Total	5 (1.00, 3♂, 2♀)	11 (1.00, 9♂, 2♀)	4 (1.00, 1♂, 3?)

Table 6. Number of known-age *P. carbo* nesting at Durell Point in 1978. The percentage of each age class and the sex ratio (when known) are in parentheses. AHY refers to *P. carbo* banded as breeding adults in 1977.

Dates	2 year	3 year	4 year	2, 3 or 4 year	AHY
10-15 April-25-30 April (pre-peak)	1 (0.14, 1♂)	0	0	0	13 (0.87, 8♂ 5♀)
1-5 May-20-25 May (peak)	2 (0.29, 1♂, 1♀)	3 (0.43, 2♂, 1♀)	6 (0.60, 4♂, 2♀)	2 (0.50, 2♀)	2 (0.13, 2♀)
26-30 May-14 June (post-peak)	4 (0.57, 2♂, 2♀)	4 (0.57, 4♂)	4 (0.40, 3♂, 1♀)	2 (0.50, 2♂)	0
Total	7 (1.00, 4♂, 3♀)	7 (1.00, 6♂, 1♀)	10 (1.00, 7♂, 3♀)	4 (1.00, 2♂, 2♀)	15 (1.00, 8♂, 7♀)

($\bar{X}$ = 4.45 ± 0.09, n = 133), although the largest number of eggs simultaneously incubated was seven. The seasonal decline in the mean clutch-size was at least partially due to the shift in a predominance of 5-egg clutches in the pre-peak period (n = 23, 63.9%) to 4-egg clutches as the season progressed (Table 7). Nevertheless, the most prevalent overall clutch-size was five eggs (n = 56, 42.1%), followed by 4- (n = 44, 33.1%) and 3- (n = 15, 11.3%) egg clutches respectively.

Eleven replacement clutches were produced at Durell Point in 1977 by *P. carbo* pairs that renested at their original site following the loss of complete (n = 4, 36.4%) or incomplete (n = 7, 63.6%) clutches, while two others were produced following the loss of chicks. Two chicks at one nest disappeared within a day of hatching while two chicks at another nest were lost at seven and 21 days respectively. *P. carbo* pairs (n = 4) that initially nested in the pre-peak period and renested during the peak period produced a mean replacement clutch-size of 5.3 ± 0.25. Post-peak period renesters (n = 8) that initially nested in the peak period produced a mean clutch-size of 3.5 ± 0.27. The replacement clutch-size of the one pair whose initial nesting attempt was in the post-peak period was unknown as observations were discontinued during the laying period due to disturbance to nearby nests.

VI. *P. carbo* Egg Fate at Durell Point in 1977

The most common cause of *P. carbo* egg loss was unknown as the eggs disappeared (n = 114, 19.3% of total, Table 8). Eggshell fragments observed on the cliff below nests suggested that some of these eggs either rolled off the cliff or broke outside the nest. The first egg laid in the

Table 7. Clutch-size distribution of *P. carbo* at Durell Point in 1977. The percentage for each clutch-size is in parentheses.

Dates	Clutch-size								Total clutches (mean ± 1 SE clutch-size)
	1	2	3	4	5	6	7	8	
12-27 April (pre-peak)	0 --	0 --	0 --	7 (19.4)	23 (63.9)	4 (11.1)	2 (5.6)	0 --	36 (5.03 ± 0.12)
28 April-14 May (peak)	0 --	1 (1.5)	6 (8.8)	25 (36.8)	32 (47.1)	2 (2.9)	1 (1.5)	1 (1.5)	68 (4.52 ± 0.11)
15 May-2 July (post-peak)	2 (6.9)	2 (6.9)	9 (31.0)	12 (41.4)	1 (3.4)	3 (10.3)	0 --	0 --	29 (3.59 ± 0.23)
Total	2 (1.5)	3 (2.3)	15 (11.3)	44 (33.1)	56 (42.1)	9 (6.8)	3 (2.3)	1 (0.75)	133 (4.45 ± 0.09)

Table 8. The fate of *P. carbo* eggs according to position in the laying sequence at Durell Point in 1977 (expressed as a percentage of the egg number in parentheses).

Egg fate	Egg Number								
	1	2	3	4	5	6	7	8	Total
hatched	40 (30.1)	67 (51.2)	78 (60.9)	67 (59.3)	38 (55.1)	8 (61.5)	3 (75.0)	0 --	301 (50.8)
disappeared	47 (35.3)	20 (15.3)	19 (14.8)	12 (10.6)	12 (17.4)	2 (15.4)	1 (25.0)	1 (100.0)	114 (19.3)
broken	19 (14.3)	18 (13.7)	9 (7.0)	11 (9.7)	4 (5.8)	1 (7.7)	0 --	0 --	62 (10.5)
rotten	16 (12.0)	10 (7.6)	10 (7.8)	12 (10.6)	5 (7.3)	0 --	0 --	0 --	53 (9.0)
addled[a]	5 (3.8)	5 (3.8)	4 (3.1)	5 (4.4)	6 (8.7)	0 --	0 --	0 --	25 (4.2)
other[b]	6 (4.5)	11 (8.4)	8 (6.3)	6 (5.3)	4 (5.8)	2 (15.4)	0 --	0 --	37 (6.3)
Total (n)	133	131	128	113	69	13	4	1	592

[a] addled refers to eggs containing visible dead embryos

[b] other refers to: no yolk, fell with nest, worker error

clutch had a significantly higher disappearance rate than that of any other eggs in the clutch (χ^2_c* = 27.21, $p < 0.001$). The first and second eggs laid in the clutch had the highest incidence of loss due to breakage, and this difference was significant against the remaining eggs in the clutch ($\chi^2_c = 5.71$, $p < 0.05$). Most (67.6%) egg loss in the disappeared and broken categories occurred following clutch completion, although some eggs (n = 57) were lost during the egg-laying stage (see below). Egg predation by gulls, crows or ravens was not observed at either colony.

Egg loss during the egg-laying stage most frequently involved only the first laid egg (n = 26), and nests which lost more than one egg generally contained above average clutches (n = 12, $\bar{X} = 5.4 \pm 0.36$). The proportion of nests that lost eggs during this stage increased with clutch-size (Table 9). Less than 50% of the clutches containing five eggs or less lost eggs before the clutch was complete while more than 50% of the larger clutches did so. The difference was significant ($\chi^2_c = 25.49$, $p < 0.001$). Another form of egg 'loss' was egg burial. Thirty-seven eggs were found embedded beneath the nest lining, but were recovered by the observer within 24 h. Egg burial appeared to occur either when the adults trod on the eggs or when fresh nest lining was placed on top of them. No eggs were found buried following the onset of full incubation. The first laid egg was most frequently buried (n = 26) while subsequent eggs were buried with decreasing frequency and no eggs after egg-3 (with the exception of one egg-4) were found buried. The proportion of nests which 'lost' eggs in this manner increased with clutch-size (Table 9). More than 50% of the clutches larger than five eggs had eggs buried while only 22 (18.3%) clutches of five eggs

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* 2 x 2 Contingency Table Chi-square, Yate's correction for continuity, (Siegel 1956)

Table 9. The effect of clutch-size on the number of *P. carbo* eggs that disappeared, broke or were buried during the egg-laying stage at Durell Point in 1977. The percentage for each clutch-size is in parentheses.

Clutch-size	Nests (n)	Nests with eggs that disappeared or broke (n)	Nests with buried eggs (n)
1	2	0	0
2	3	0	0
3	15	2 (13.3)	1 (6.7)
4	44	7 (15.9)	5 (11.4)
5	56	21 (37.5)	16 (28.6)
6	9	8 (88.9)	5 (55.6)
7	3	3 (100.0)	2 (66.7)
8	1	1 (100.0)	1 (100.0)
Total	133	42 (31.6)	30 (22.6)

or less did so (χ^2_c = 15.13, $p < 0.001$). Fourteen (37.8%) recovered eggs subsequently hatched and 12 (85.7%) of the chicks fledged. Egg replacement did not influence either the hatching or fledging success trends reported.

VII. Incubation Period and Hatching Interval

Incubation period is defined here as the interval from the laying of the last egg of a clutch to the hatching of that egg on the assumption that incubation behaviour is fully established by the time the last egg is laid (Drent 1975). The mean incubation period for 74 *P. carbo* eggs laid last in the clutch at Durell Point in 1977 was 29.3 ± 0.10 days. However, the number of days that eggs were present in the nest before hatching ranged from 27-38 days. Mean pre-hatching periods for eggs in 3-, 4- and 5-egg clutches throughout the breeding season are in Table 10. The number of days that an egg remained in the nest before hatching was inversely related to its position in the laying sequence (Table 10).

It was not possible to determine exactly when adult *P. carbo* began incubating their eggs. Full incubation did not begin with the laying of the first egg as it was not until at least after the second egg was laid, and sometimes even later, that the eggs felt warm to touch. In 3-, 4- and 5-egg clutches the second last and/or last eggs laid generally hatched within 29-30 days while earlier laid eggs took progressively longer (Table 10).

The hatching interval of all eggs in a clutch increased with clutch-size, although sample sizes were too low for meaningful statistical analysis. In clutches where all of the eggs hatched, 3-egg clutches (n = 4) averaged 3.3 days while 4- (n = 10) and 5- (n = 2) egg clutches averaged 4.2 and 4.5 days respectively. Upon hatching, *P. carbo* chicks weighed

Table 10. Pre-hatching period (in days) for *P. carbo* eggs in 3-, 4- and 5-egg clutches at Durell Point in 1977.

Clutch size	Egg laying order				
	1	2	3	4	5
3					
$\bar{X}$	33.3	31.0	29.1	--	--
S.E.	0.68	0.76	0.23	--	--
n	7	8	8	--	--
4					
$\bar{X}$	33.8	31.4	29.9	29.5	--
S.E.	0.28	0.20	0.20	0.18	--
n	19	23	25	24	--
5					
$\bar{X}$	35.2	33.3	31.2	29.9	29.2
S.E.	0.66	0.21	0.16	0.15	0.17
n	11	27	37	31	30

less than 2% of the adult's body weight (Table 11, c♂. Appendix I). There was relatively little variation in weight among newly hatched chicks, although the difference increased with chick age (Fig. 11).

VIII. Hatching Success of *P. carbo* Eggs.

Hatching success was measured as the number of chicks hatched per egg laid. The mean hatching success for different clutch-sizes and for all clutch-sizes pooled at Durell Point throughout the 1977 season are in Table 12. The hatching success of all clutch-sizes pooled declined from 0.60 eggs hatched per egg laid in the pre-peak period to 0.52 and 0.39 eggs hatched per egg laid in the peak and post-peak periods respectively. Eggs laid during the post-peak period had a significantly lower mean hatching success than those laid in the peak ($\chi^2_c = 5.01$, $p < 0.05$) and pre-peak ($\chi^2_c = 11.55$, $p < 0.001$) periods. However, no difference ($\chi^2_c = 2.82$, $p > 0.10$) between the eggs laid during the pre-peak and peak periods was found.

In most cases there was only slight within clutch-size variation in hatching success as the season progressed. Generally, all clutch-sizes exhibited a similar decrease in the hatching success over the season (Table 12). The only significant decrease was observed in 6-egg clutches in post-peak period against the pre-peak (Fisher Test, $p = 0.0013$) and peak (Fisher Test, $p = 0.0022$) periods.

All clutch-sizes where eggs hatched had a similar overall hatching success. However, during the post-peak period clutches larger than four eggs had a hatching success (0.13 eggs hatched/egg laid) significantly lower than the remaining clutches (0.46 egg hatched/egg laid; $\chi^2_c = 6.74$ $p < 0.01$).

Table 11. Mean daily weight of *P. carbo* chicks from 4- and 5-egg clutches at Durell Point in 1977.

Age (days)	Chicks (n)	Weight (g) (mean)	± 1 S.E.
1	102	48.5	0.70
2	67	58.7	1.17
3	81	72.7	1.51
4	59	95.5	2.39
5	67	124.4	3.03
6	62	167.5	4.81
7	63	215.2	4.98
8	50	266.0	7.33
9	57	350.3	11.04
10	47	430.8	13.28
11	37	522.8	15.53
12	48	639.3	15.99
13	39	762.7	15.39
14	41	871.7	19.66
15	31	973.2	30.04
16	31	1144.8	31.55
17	36	1245.4	30.41
18	28	1347.9	30.75
19	31	1462.9	34.67
20	29	1679.0	39.18
21	24	1751.3	37.72
22	22	1828.2	48.82
23	15	1907.3	54.74
24	14	1927.9	58.63
25	7	2033.4	72.79
26	6	2190.0	122.48

Figure 11. Mean daily weight and standard deviations of *P. carbo* chicks from 4- and 5-egg clutches at Durell Point in 1977.

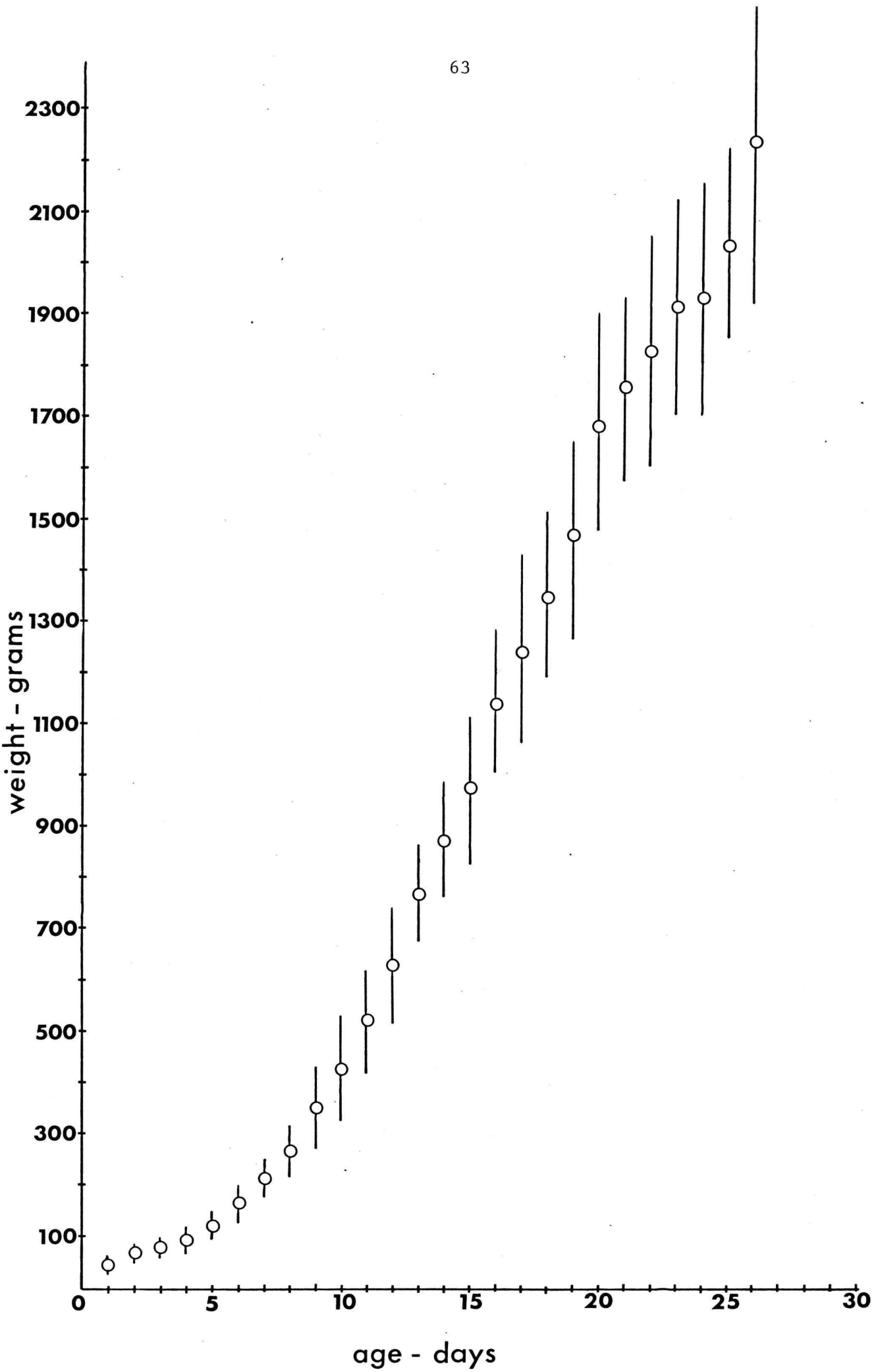

2300
2100
1900
1700
1500
1300
1100
900
700
500
300
100
weight - grams
0
5
10
15
20
25
30
age - days

Table 12. The hatching success of *P. carbo* eggs laid at Durell Point in 1977. All nests are included except renesting attempts and those lost accidentally.

Clutch- size	nests (n)			eggs laid			eggs hatched per egg laid			Total
	prepeak	peak	postpeak	prepeak	peak	postpeak	prepeak	peak	postpeak	
1	0	0	2	--	--	2	--	--	0	0
2	0	1	2	--	2	4	--	0	0	0
3	0	5	9	--	15	27	--	0.60	0.52	0.55
4	7	25	12	28	100	48	0.57	0.59	0.48	0.56
5	22	31	1	110	155	5	0.60	0.50	0	0.53
6	4	2	3	24	12	18	0.67	0.58	0.17	0.48
7	2	1	0	14	7	--	0.57	0.43	--	0.52
8	0	1	0	--	8	--	--	0	--	0
Total	35	65	29	176	299	104	0.60	0.52	0.39	0.52

IX. Brood-Size and Chick Loss

A brood is defined as "collectively, the young hatched from a single clutch of eggs" (Thomson 1964, p. 110). The mean *P. carbo* brood-size for the whole season at Durell Point in 1977 was 2.32 ± 0.13 chicks per nest. During the pre-peak period the mean brood-size was 3.06 ± 0.18 chicks per nest and decreased to 2.36 ± 0.18 and 1.32 ± 0.28 chicks per nest during the peak and post-peak periods respectively. The relationship between clutch-size and brood-size is in Table 13. As clutch-size increased there was a corresponding increase in the mean brood-size, except in clutches where no eggs hatched. The most prevalent overall brood-size was three chicks (n = 36) and it was generally the most common brood-size for each clutch-size.

The loss distribution of *P. carbo* chicks relative to brood-size at Durell Point in 1977 is in Table 14. Significantly more chicks survived from 3-, 4- and 5-chick broods than from 1- and 2-chick broods ($\chi^2_c = 4.74$, $p < 0.05$). In all brood-sizes combined, half of all chick loss occurred during the first five days after hatching. There was then a rapid decrease in subsequent loss with age (Fig. 12). The most frequent category of chick loss was chick mortality at the nest from unknown causes (n = 35, 61.4%). Chicks that disappeared (n = 16, 28.1%) were presumed dead from falling off the cliff or from predation. From 23 July 1976 until the end of the 1976 field season an immature Bald Eagle (*Haliaeetus leucocephalus*) remained in the vicinity of the Durell Point colony. During this time, approximately 25 *P. carbo* chicks (three-six weeks old) disappeared from their nests. The eagle was often perched in the trees above the colony or on the cliff amidst the cormorant nests. The loss of these chicks was attributed to eagle

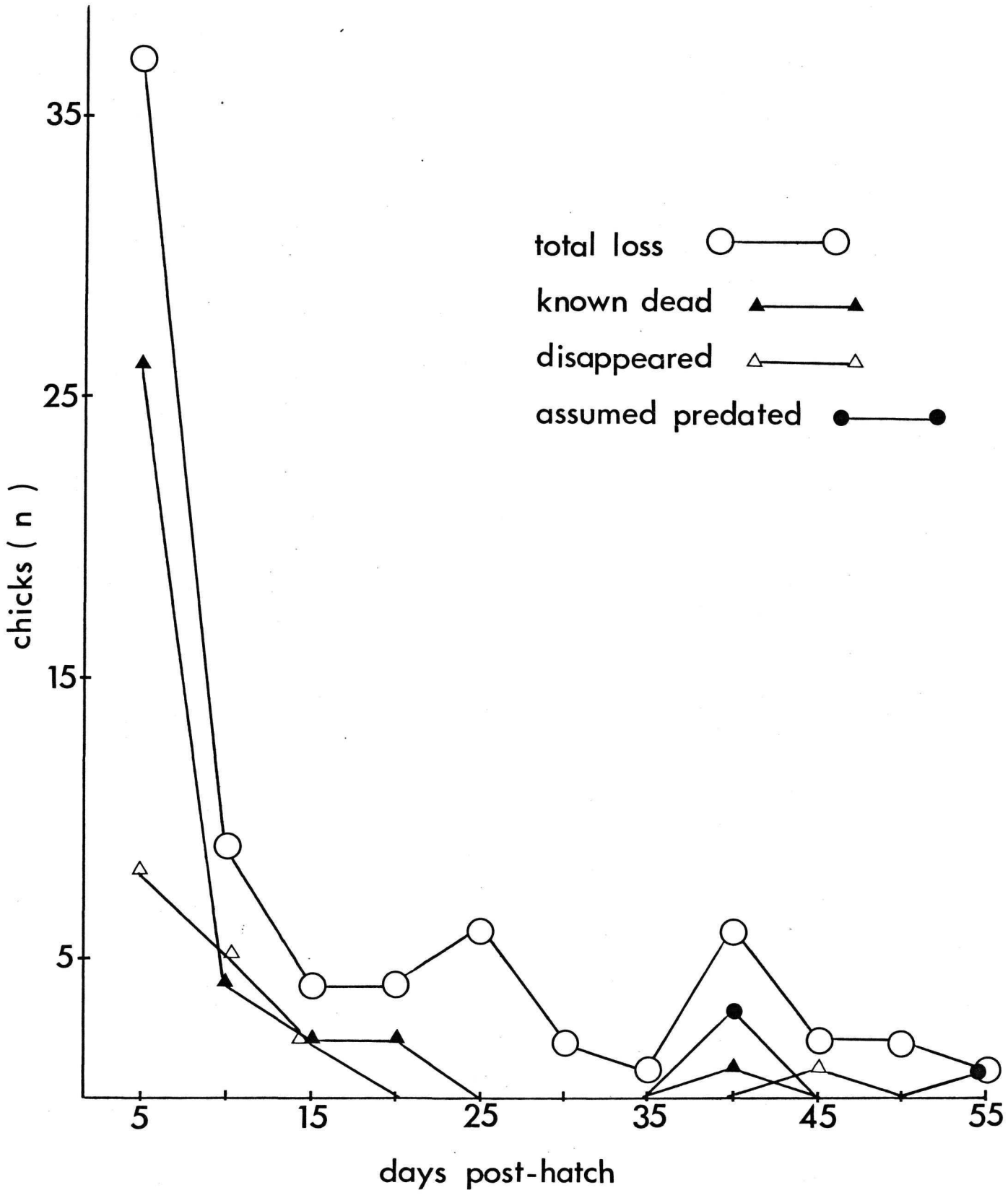
Table 13. *P. carbo* broods hatched according to clutch-size at Durell Point in 1977. Renesting attempts and clutches from nests accidentally lost prior to hatching are not included. Percentage of each clutch-size is in parentheses.

Clutch-size	Clutches (n)	Brood-size									$\bar{X}$ brood-size ± 1 S.E.
		0	1	2	3	4	5	6	7	8	
1	2	2 (100)	0	--	--	--	--	--	--	--	0
2	3	3 (100)	0	0	--	--	--	--	--	--	0
3	14	3 (21.4)	4 (28.6)	2 (14.3)	5 (35.7)	--	--	--	--	--	1.64 ± 0.32
4	44	7 (15.9)	6 (13.6)	11 (25.0)	10 (22.7)	10 (22.7)	--	--	--	--	2.23 ± 0.21
5	54	6 (11.1)	5 (9.3)	10 (18.5)	16 (29.6)	15 (27.8)	2 (3.7)	--	--	--	2.64 ± 0.19
6	9	2 (22.2)	0	0	4 (44.4)	1 (11.1)	2 (22.2)	0	--	--	2.89 ± 0.61
7	3	0	0	0	1 (33.3)	2 (66.7)	0	0	0	--	3.67 ± 0.33
8	1	1 (100)	0	0	0	0	0	0	0	0	0
Total	130	24 (18.5)	15 (11.5)	23 (17.7)	36 (27.7)	28 (21.5)	4 (3.1)	0	0	0	2.32 ± 0.13

Table 14. *P. carbo* chick loss according to brood-size at Durell Point in 1977.

	Brood-size				
	1	2	3	4	5
n	15	23	36	28	4
chicks (n)	15	46	108	112	20
chicks lost (n)	5	12	20	17	3
chicks lost/hatched	0.33	0.26	0.19	0.15	0.15

Figure 12. Loss distribution of *P. carbo* chicks at Durell Point in 1977.


35
25
15
5
chicks (n)
total loss
known dead
disappeared
assumed predated
5
15
25
35
45
55
days post-hatch

predation, although no actual encounters were seen. On 8 August 1977 an immature Bald Eagle appeared at this colony and remained in the vicinity until the end of the field season. Five large *P. carbo* chicks disappeared from their nests during this time, although no evidence of eagle predation was observed. No evidence of chick predation at the nest by gulls, crows, ravens or land predators was observed throughout this study.

The most frequent category of *P. carbo* chick loss at Cape Tryon in 1976 was disappearance at both cliff-face (n = 17, 68%) and cliff-shelves nests (n = 15, 79%). Chicks that disappeared from cliff-face nests were assumed to have fallen off the ledges as these sites were inaccessible to land predators and no avian predators capable of taking large chicks (*e.g.*, Bald Eagle) were observed. Chicks that disappeared from the cliff-shelves were assumed to have either fallen off the cliff or been taken by land predators. Red Foxes (*Vulpes fulva*) were believed to have killed at least three *P. carbo* chicks found partially consumed above the cliff in 1976, as a trail in the grass led to the most accessible nests. Fresh digging into Bank Swallow nests and an abandoned den near the colony were further evidence of fox activity. No evidence of gull, crow or raven predation on cormorant chicks was recorded. At least five half-grown *P. carbo* chicks at cliff-face nests were forcibly evicted by site-seeking adult *P. auritus* in 1976. *P. auritus* chicks that disappeared from cliff-face nests were assumed to have fallen off their ledges, although several instances of aggressive interactions between half-grown chicks and adult *P. auritus* suggested that some chicks may have been forcibly evicted. In addition, severe storms (*e.g.*, 12 June 1976) sometimes swept away nests and contents from the cliff-base and lower cliff-face ledges.

X. Fledging Success

Cormorant chicks that flew from their nests on the cliff or in the trees were considered fledged. *P. carbo* chicks generally joined communal roosting areas used by the adults at the water's edge when between 50 and 56 days post-hatch, while *P. auritus* chicks did so at 45-50 days post-hatch. *P. carbo* and *P. auritus* chicks were incapable of flight prior to 45 and 40 days respectively. Hence, chicks that disappeared before then were not considered fledged.

Fledging success is defined as the number of chicks fledged per egg hatched. A more complete measure of the total reproductive success is the number of chicks fledged per egg laid. However, where the nests' contents could not be observed until chicks were present, total reproductive success was measured as the number of chicks fledged per nest. At Cape Tryon and Durell Point in 1976 and at Cape Tryon in 1977, the majority of chicks were not observed until they were at least one week post-hatch, by which time most chick mortality had likely occurred (cf. Fig. 12).

The number of chicks fledged per nest by *P. carbo* and *P. auritus* at Cape Tryon in 1976 and 1977 is in Tables 15 and 16 respectively. No difference was found between *P. carbo* nesting on the cliff-face and those nesting on the cliff-shelves in 1976 and 1977 (χ^2_c 2.49, $p > 0.10$ and $\chi^2_c = 3.45$, $p > 0.05$ respectively) although in both years pairs nesting on the cliff-shelves fledged more chicks per nest than those nesting on the cliff-face (Table 15). Success was higher for both species at Cape Tryon in 1976 that in 1977 except for the *P. auritus* at the cliff-base in 1976. Most *P. auritus* nests at the cliff-base were swept away in a storn 12 June 1976.

Table 15. Reproductive success of *P. carbo* at Cape Tryon in 1976 and 1977. Majority of chicks were not observed until at least one week post-hatch.

Year	Nests (n)	Chicks (n)	Chicks per nest (mean)	Chicks fledged (n)	Chicks fledged per nest (mean)
1976					
cliff-face	35	94	2.7	69	1.97
cliff-shelves	43	104	2.4	85	1.98
total	78	198	2.5	154	1.97
1977					
cliff-face	40	66	1.7	53	1.33
cliff-shelves	87	174	2.0	154	1.77
total	127	240	1.9	207	1.63

Table 16. Reproductive success of *P. auritus* at Cape Tryon in 1976 and 1977. Majority of chicks were not observed until at least one week post-hatch.

Year	Nests (n)	Chicks (n)	Chicks per nest (mean)	Chicks fledged (n)	Chicks fledged per nest (mean)
1976					
cliff-face	98	262	2.7	224	2.29
cliff-base	63	0	0	0	0
total	161	262	1.6	224	1.39
1977					
cliff-face	93	215	2.3	201	2.16
cliff-base	52	31	0.6	31	0.60
total	145	246	1.7	232	1.60

The fledging success of *P. carbo* at Durell Point in 1977 was 0.82 chicks fledged per egg hatched and 0.43 chicks fledged per egg laid (Table 17). There were 1.61 *P. carbo* chicks fledged per nest in 1977 compared with 1.79 chicks fledged per nest in 1976. *P. auritus* fledged 2.00 and 1.20 chicks per nest at Durell Point in 1976 and 1977 respectively. The fledging success of *P. carbo* in 1977 declined only during the post-peak period although not significantly compared with the pre-peak and peak periods ($\chi^2_c = 1.41$, $p > 0.20$; $\chi^2_c = 1.73$, $p > 0.10$ respectively). The seasonal decline in the number of chicks fledged per egg laid reflected the hatching success with significant differences between the post-peak versus the pre-peak and peak periods ($\chi^2_c = 12.25$, $p < 0.001$; $\chi^2_c = 6.91$, $p < 0.01$ respectively). Three-egg clutches fledged relatively few chicks compared with larger clutch-sizes (Table 17). The differences in fledging success between 3-egg clutches versus 4-, 5- and 6-egg clutches were significant ($\chi^2_c = 11.90$, $p > 0.001$; $\chi^2_c = 9.01$, $p > 0.01$; $\chi^2_c = 8.13$, $p > 0.01$ respectively), although there was no difference between 3- and 7-egg clutches (Fisher Test, $p = 0.11$). In addition, 3-chick broods hatched from 3-egg clutches fledged significantly fewer chicks than 3-chick broods hatched from 4-, 5- and 6-egg clutches ($\chi^2_c = 7.52$, $p > 0.01$). No significant differences in fledging success were found between any of the other clutch-size combinations.

Table 17. Fledging success of *P. carbo* at Durell Point in 1977. All pairs are included except renesters and those that lost nests accidentally prior to the eggs hatching.*

Clutch-size	nests (n)			chicks fledged (n)			chicks fledged per egg hatched			chicks fledged per egg laid			chicks fledged per nest (total)
	prepeak	peak	postpeak	prepeak	peak	postpeak	prepeak	peak	postpeak	prepeak	peak	postpeak	
1	0	0	2	--	--	--	--	--	--	--	--	0	0
2	0	1	2	--	--	--	--	--	--	--	0	0	0
3	0	5	9	--	5	8	--	0.56	0.57	--	0.33	0.30	0.93
4	7	25	12	16	49	19	1.00	0.83	0.83	0.57	0.49	0.40	1.91
5	22	31	1	52	65	0	0.79	0.84	0	0.47	0.42	0	2.17
6	4	2	3	14	7	2	0.88	1.00	0.67	0.58	0.58	0.11	2.56
7	2	1	0	6	3	--	0.75	1.00	--	0.43	0.43	--	3.00
8	0	1	0	--	0	--	--	0	--	--	0	--	0
Total	35	65	29	88	129	29	0.83	0.83	0.73	0.50	0.43	0.29	1.91

* See Appendix IX for comparative data from other cormorant studies.

DISCUSSION

A. Age-Related Breeding Activities by *P. carbo*

Most bird studies have been conducted on populations where the age of the study animals is unknown. As data from studies containing marked, known-age birds accumulate, it is evident that many species exhibit similar age-related phenomena. In this study I was fortunate to work with a population of *P. carbo* where several age classes were known. It is my intention in this section to show that *P.* c. *carbo* may also exhibit some of the same age-related phenomena demonstrated elsewhere for other species (cf. Richdale, 1951,1957; Coulson and White 1958, 1960; Potts 1966). In addition, I will utilize these data to suggest ways in which age may be a factor that influences the nesting distribution of *P. carbo* and *P. auritus* at Cape Tryon.

While individuals of most bird species exhibit a characteristic age of first breeding, it has frequently been observed that some individuals breed earlier and that the number breeding in successive years increases until the characteristic age is reached (Richdale, 1954; Austin and Austin 1956; Johnston 1956). When breeding occurs earlier than the characteristic age, it has often been associated with particularly favorable conditions (Lack 1968; Braithwaite and Clayton 1976). Potts (1966) observed that two year old *P. aristotelis* did not breed in colonies where numbers were stable, but that breeding two year olds were found in expanding populations. The characteristic age of first breeding in *P. carbo sinensis* is normally four to five years (Kortlandt in Cramp *et al.* 1977). However, *P. carbo* were

observed breeding as two year olds at Durell Point during each year of this study with a subsequent increase in the number of breeders with age. In addition, one female was observed breeding in 1976 while still in the plumage of a first-year immature bird. Frequent vandalism (*i.e.*, shooting) at the Durell Point colony prior to the late 1960's or early 1970's (Erskine 1972) may have been responsible for keeping this colony below the potential carrying capacity for nest sites at the colony. Following a reduction in vandalism in the 1970's (J. MacKenzie pers. comm.), however, conditions apparently became more stable which permitted colony expansion. As the colony spread on to the adjacent cliffs additional nest sites became available, possibly to young birds that were unable to aquire nest sites previously. A similar situation is reported for one-year old male Red-winged Blackbirds (*Agelaius pheoniceus*) that claimed territories and bred when adult (older) males were experimentally removed (Lack 1968). While an early onset of maturity may be important for species with short reproductive lives (*e.g.* many small passerines) this is not likely the case for long-lived birds (Lack 1968). *P. carbo* are long-lived birds (record 19 years, 8 months, Rydzewski in Cramp *et al.* 1977). Thus, there would appear to be no strong selective pressure to evolve early maturity, although, if conditions permit, breeding may occur earlier than normal.

Another age-related phenomenon frequently observed among birds is that younger individuals nest later in the season than older individuals. This has been shown clearly in such diverse species as *P. aristotelis* (Potts 1966), Black-legged Kittiwakes (*Rissa tridactyla*, Coulson and White 1958, 1960) and Blue Grouse (*Dendragapus obscurus*, Zwickel 1977). The reasons for this may be complex and varied but are thought to involve such age-specific

factors as differences in physiological maturity, foraging abilities and possible intraspecific interference with experienced breeders (Zwickel 1977). I obtained evidence that these age-related phenomena also occur in *P. carbo*. At Durell Point, no known-age two or three year old *P. carbo* were included among the 50 *P. carbo* pairs with clutch-starts in April 1977. However, 20 known-age two and three year olds had clutch-starts following 1 May 1977. Most (n = 8) of the marked three-year olds nested between 2 and 14 May 1977, whereas most (n = 4) of the marked two-year olds nested between 15 May and 2 July 1977. Similarly, 27 marked two, three and four year old *P. carbo* in 1978 had clutch-starts in May, although one individual (a two-year old male) may have nested earlier. Thus, the clutch-start chronology of *P. carbo* at Durell Point appeared to be related to the age of the individuals involved. Potts (1966) observed progressively earlier nesting dates with increased age in *P. aristotelis* and observed that early nesting birds occupied the best nest sites available. Thus, the marked adults (n = 9) of unknown age that nested in April 1977 and 1978 at Durell Point are suspected to have been older than three or four years as no known-age birds of this age or younger nested at that time.

Many birds return to the general vicinity of their natal location to breed (Thomson 1964). In some species, individuals are strongly attached to former nesting territories. Such site tenacity apparently increases with age and with each additional occupancy of the nest site (Welty 1962). *P. carbo* at Durell Point exhibited a marked tendency to return to their natal colony to breed although some inter-colony movements were observed. The full extent of these movements was unknown as a result of limited observations made at other colonies. While site tenacity is usually more

highly developed in cliff-nesting, colonial birds (McNicholl 1975) mudslides on certain parts of the cliff at Durell Point in 1977 may have forced some birds to seek new sites elsewhere. Potts (1966) associated a change of nest site in *P. aristotelis* with nesting failure and noted that females changed sites more frequently than males. Although the sex of the marked *P. carbo* observed at the Chepstow and McKinnon Point colonies in 1977 and 1978 was unknown, it is possible that they were females that nested unsuccessfully at Durell Point the year before.

B. Nest Site Selection by *P. carbo* and *P. auritus*

It is not my intention to elaborate on competition theory (cf. Miller 1967) as a detailed knowledge of the extent of niche overlap between *P. carbo* and *P. auritus* is unavailable. However, preliminary evidence suggests that interspecific competition for nest sites occurred between the two species at the Cape Tryon colony. This is based on the observation that certain cliff-face ledges were exchanged between individual pairs of the two species from one year to the next. Information on the arrival chronology, habitat usage, and date of nest site occupation according to age of individuals of the two species may suggest factors influencing the outcome of nest site competition between them. As noted by Lack (1968), nest site competition at seabird colonies (intraspecific and interspecific) is often intense as suitable colony sites are frequently restricted. Cape Tryon is the only cormorant colony on the north shore of Prince Edward Island (cf. Fig. 1).

The total time period of nest site occupancy by *P. carbo* and *P. auritus* individuals at Cape Tryon in 1977 was spread over approximately three months (March-May). The peak of nest site occupation by *P. carbo*

on the cliff-face was approximately one month earlier than that on the cliff-shelves. The reasons for this pronounced difference are unclear, although the age of the individuals involved may be a factor. Unfortunately, there were no known-age *P. carbo* nesting at Cape Tryon during this study. However, as noted previously, the earliest nesting individuals were suspected to be older than later-nesting birds. The exposed cliff-shelves apparently became available as nesting habitat in the late 1960's or early 1970's following a reduction in vandalism (*i.e.*, shooting, local residents, pers. comm.) at the colony. Many of the *P. carbo* that subsequently occupied this habitat were possibly young birds that were previously unable to attain a site on the cliff-face. As noted previously for *P. carbo* at Durell Point, colony expansion at this time may have been due, in part, to an increase in breeding by young birds. Another explanation may involve nest site competition with *P. auritus*. While many *P. carbo* individuals occupied nest sites earlier than *P. auritus* individuals, there was a period of approximately six weeks when individuals of both species were occupying nest sites. The first sites chosen by both *P. carbo* and *P. auritus* adults were broad cliff-face ledges. Hence, the early nesting (older?) *P. auritus* (April) that occupied potential *P. carbo* nest sites prior to the nest site occupation by young *P. carbo* may have forced the latter to nest elsewhere (the cliff-shelves). Because *P. auritus* individuals are smaller and build a less bulky nest, they are able to utilize smaller ledges. However, such nest sites were generally occupied only after there were no broad ledges available.

Competition for cliff-face ledges among other seabird species has been observed elsewhere. Common (*Uria aalge*) and Thick-billed (*U. lomvia*) murres compete for these nest sites (Williams 1974), as do Red-legged

(*Rissa brevirostris*) and Black-legged Kittiwakes (Kenyon and Phillips, 1965) and Black-legged Kittiwakes and Fulmars (*Fulmaris glacialis*, Coulson and Horobin 1972). Evidence that competition for nest sites occurs at Cape Tryon is further supported by differences in the arrival chronology of *P. auritus* at Cape Tryon and Durell Point. *P. auritus* returned to Durell Point more than two weeks later than at Cape Tryon in 1977. This may be related to nest site availability, colony size or to the age of the birds (see Palmer 1962). When *P. auritus* returned to Durell Point in 1977, their sites from the previous year were vacant as *P. carbo* did not nest in trees at Durell Point during this study. Furthermore, as tree nest sites were abundant, there may have been less pressure to arrive early to obtain a nest site. No *P. auritus* pairs constructed nests on the concrete blocks at Durell Point. The reasons for this are uncertain, although an abundance of arboreal nest sites, and the tendencies to occupy familiar nesting habitat first and/or to associate with conspecifics are likely factors. In contrast, late nesting *P. auritus* at Cape Tryon were able to obtain nest sites at the cliff-base only, as all cliff-face sites were occupied. Cliff-nesting Black-legged Kittiwakes return earlier to colonies of high density where sites may be more difficult to obtain (Coulson and White 1960). This has also been observed among cliff-nesting Fulmars (Fisher 1952).

C. Seasonal Variation in *P. carbo* Breeding Success (Durell Point)

A study of seasonal variation in breeding success requires that a comparison be made among subsets of the total amount of data collected throughout the breeding season. As the breeding season is generally

continuous from beginning to end, any division of it for the sake of comparisons may be considered artificial. Various split-dates may result in the data yielding similar (or dissimilar) trends. However, the split-dates chosen should provide meaningful comparisons that are biologically sound.

Snow (1960) examined seasonal variation in the breeding success of *P. aristotelis* on a weekly basis. Potts (1966) made reference to seasonal differences in breeding parameters in terms of early and/or late nesters. However, neither Snow (1960) not Potts (1966) acquired precise clutch-start dates for *P. aristotelis* as daily visits to the colonies were not made. The present work is unique among cormorant studies in that it provides the precise clutch-start dates for virtually all pairs in the colony. Consequently, the clutch-start chronology of *P. carbo* at Durell Point in 1977 was used to determine split-dates for examination of seasonal variation in breeding success.

I suggested earlier that age may influence the time of breeding by *P. carbo* individuals at Durell Point. Chardine (1978) observed that many of the late-breeding Ring-billed Gull (*Larus delawarensis*) individuals at a colony on Lake Ontario were in subadult plumage. No subadult birds were observed breeding during the earlier, main phase of nesting activity. Potts (1966) found that the median laying date (the date by which 50% had laid) of *P. aristotelis* females occurred progressively later in the season for younger birds such that the oldest and youngest breeders had median laying dates more than one month apart. Thus, the majority of birds within a particular age class could be expected to lay within a defined time period.

The factors that produced the three major peaks of nesting activity among *P. carbo* at Durell Point in 1977 are unclear. However, social stimulation among individuals at the same stage of physiological readiness may be involved (Orians 1961; Hailman 1964; Yom-Tov 1975). In any case, the three peak periods were believed to contain sufficiently distinct age groups to justify comparisons of breeding success between them. The 28 April-14 May period likely contained the greatest variation of age groups. However, the early and late peak periods were suspected to contain a proportionately greater number of older and younger birds respectively.

At Durell Point in 1977 the mean clutch-size of *P. carbo* declined as the breeding season progressed. This was largely due to the absence of small clutch-sizes (less than four eggs) during the pre-peak period and the scarcity of large clutch-sizes (more than four eggs) during the post-peak period. Seasonal declines in clutch-size have been reported for many species (Weidmann 1964). Snow (1960) suggested that this was likely not due to a shortage of food at the time of laying as smaller clutches were laid when the early breeders were feeding their young. While some species apparently show a relationship between clutch-size and age (Richdale 1957) it could not be established if this were true for *P. carbo*. Only four known-age *P. carbo* females nested at Durell Point in 1977 and complete histories of clutch-sizes were unavailable in 1978. Nevertheless, the observation that most marked three and two year old *P. carbo* nested primarily during the peak and post-peak periods in 1977 respectively, at a time when clutch-size progressively declined, suggests that age and clutch-size may be related. As noted correctly by Welty (1962), there are many

variables that may influence clutch-size. Thus, it is risky to suggest, with certainty, which factor is of primary importance.

While *P. carbo* that nested during the pre-peak and peak periods had similar hatching and fledging success, those that nested during the post-peak period exhibited a significantly lower hatching success compared to that of the earlier periods. However, fledging success among the post-peak nesters did not differ significantly from those that nested earlier. Similarly, Snow (1960) found that *P. aristotelis* pairs that nested during the first three or four weeks of the onset of breeding showed approximately the same rate of success, whereas fifth and sixth week nesters showed less success and the seventh and eighth week nesters very little. At Durell Point in 1977, the end of the fourth week coincided with the end of the peak period. The fifth and sixth weeks contained most of the pairs that nested during the post-peak period. Snow (1960) attributed the low breeding success late in the season to the young age of individuals breeding then. While a similar explanation may hold for *P. carbo* at Durell Point, precise reasons are unknown. To distinguish between the influence of season and age upon reproductive success, it is necessary to observe several known age classes nesting at different times of the breeding season. Unfortunately, this was not possible during this study. As noted by Potts (1966), the earlier that *P. aristotelis* individuals occupied nest sites, the better was the probability of successful breeding. While late nesting *P. auritus* occupied suboptimal locations at Cape Tryon (cliff-base), the trend was less obvious among late nesting *P. carbo*. The reasons why hatching success but not fledging success of the post-peak period nesters should decline significantly are puzzling. A similar trend

has been observed in some Larids (R. D. Morris, pers. comm.). Possibly post-peak period nesters are more inclined to neglect their eggs but less inclined to neglect their chicks. Cormorants at my colonies became increasingly wary as chicks began to fledge and the number of birds remaining at the colony decreased. Even individuals that were 'bold' at the peak of the season became 'shy' later on. Snow (1960) recorded a similar observation for *P. aristotelis* individuals.

Seasonal variation in nesting success was not examined at Cape Tryon during this study. However, *P. carbo* that nested on the cliff-shelves in 1976 and 1977 fledged more chicks per nest than those on the cliff-face. A possible reason for this was that chicks from cliff-face nests were more susceptible to falling off the cliff. *P. auritus* nesting on the cliff-face fledged more chicks per nest in 1976 and 1977 than *P. carbo* on either habitat. *P. auritus* chicks are smaller than *P. carbo* chicks and thus they may have been less likely to fall from their nests.

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Appendix I. Weight (g) and beak measurements (mm) of adult *P. carbo* captured at Durell Point in 1977. Weight was taken to the nearest 50 grams. Individuals belonging to the same pair are indicated and the sex of each bird is recorded (when known).

Weight (g)	Beak length (mm)	Beak depth (mm)	Sex
[3600	74.6	23.5	♂
[3100	68.4	21.8	♀
[3850	75.9	24.2	♂
[3000	68.5	21.7	♀
[3400	75.3	23.7	♂
[2600	65.5	21.2	♀
[3750	74.4	25.7	♂
[3000	66.1	23.7	♀
[3200	71.3	24.1	♂
[2800	67.9	22.8	♀
[3400	79.1	26.4	♂
[3100	68.6	22.8	♀
[3900	75.6	23.7	♂
[2850	73.2	23.8	♀
[4100	76.0	24.0	♂
[3250	72.6	21.4	♀
[3900	77.2	22.3	♂
[2700	66.8	20.4	♀
[3700	73.8	23.9	♂
[2900	72.2	22.1	♀
3250	78.1	26.8	
3700	83.8	27.4	
3850	77.1	25.9	
3550	77.2	25.1	
3550	72.3	24.7	
3500	76.1	23.2	
3800	83.7	24.4	
3800	80.9	26.5	
2850	67.0	23.4	
2900	71.7	23.8	
3550	74.1	28.2	
[3700			♂
[3000	68.2	18.8	♀

[a] pair killed when rock fell on their cliff-shelf nest at Cape Tryon; specimens presently in National Museum, Ottawa.

Appendix II. Known mixed species colonies of *P. carbo* and *P. auritus*.

Location	*P. carbo* pairs (n)	*P. auritus* pairs (n)	Date	Source
Cape Tryon, Prince Edward Island	150	403	1978	pers. obs. (Hogan)
Durell Point, Prince Edward Island	161	20	1978	pers. obs. (Hogan)
Blue Gull Rock, Nova Scotia	20-30	400-430	1971	Lock and Ross (1973)
Green Island, Nova Scotia	30-35	240-250	1971	Lock and Ross (1973)
Eastern Basque Island, Nova Scotia	95-100	20-25	1971	Lock and Ross (1973)
Rock NW of Fourchu Head, Nova Scotia	30-50	65-85	1971	Lock and Ross (1973)
Sugarloaf Island, Nova Scotia	160-180	15-20	1971	Lock and Ross (1973)
NW St. Pierre Island (France)	16	+	1963 or 1964	Cameron in Brown *et al.* (1975)
Petite Miquelon Island (France)	>20	8	1964	Cameron in Brown *et al.* (1975)
Cliff Island, Quebec	98	21	1977	pers. comm. G. Chapdelaine
East Island, Quebec	9	40	1977	pers. comm. G. Chapdelaine
Percé Rock, Quebec	18	341	1976	pers. comm. G. Chapdelaine
High Bank, Prince Edward Island[a]	241	9	1977	pers. obs. (Hogan)
Crystal Cliffs, Nova Scotia[a]	+	+	1937-1941	Erskine (1972)
Hertford Island, Nova Scotia[a]	39	+	1940	Tufts in Erskine (1972)

[a] colonies now contain only *P. carbo*

Appendix III. Known number of nests of both cormorant species at Durell Point from 1952 to 1978. The dates of the nest counts are in parentheses.

Year	*P. carbo*	*P. auritus*	Source
1952	19+ (3 June-13 July)	0	Godfrey 1954
1960	40+ (23 April)	0	MNR[a] (Erskine, Bartlett)
1960	60 (13 July)	0	MNR (Erskine van Tets)
1963	27 (8 June)	0	MNR (Pigot)
1964	26 (28 June)	0	MNR (Pigot)
1966	64 (5 June)	0	MNR (Pigot)
1974	110 (5 June)	0	Hogan (pers. obs.)
1975	162 (16 June)	14 (16 June)	Hogan (pers. obs.)
1976	186 (23 April-11 Sept)	15 (23 April-11 Sept)	Hogan (pers. obs.)
1977	153 (21 March-1 Sept)	12 (21 March-1 Sept)	Hogan (pers. obs.)
1978	161 (27 May-14 June)	20 (27 May-14 June)	Hogan (pers. obs.)

[a] Maritime Nest Records Scheme. Canadian Wildlife Service, Sackville, N.B.

Appendix IV. Known number of nests of both cormorant species at Cape Tryon from 1936 to 1978. The dates of the nest counts (where available) are in parentheses.

Year	*P. carbo*	*P. auritus*	Source
1936	colony occupied		Peters in Erskine 1972
1941	25 (11 June)	75 (11 June)	Peters 1942
1942	both species		Peters in Erskine 1972
1943	both species		Peters in Erskine 1972
1944	both species		Peters in Erskine 1972
1945	both species: 300-350 nests		Peters in Erskine 1972
1952	35 (17 July)	87 (17 July)	Godfrey 1954
1960	36 (11 July)	108 (11 July)	MNR[a] (Erskine van Tets)
1963	both species (21 July)		MNR (Thomas)
1964	both species (7 June)		MNR (Vass)
1965	both species (27 June)		MNR (Pigot)
1967	24 (2 July)	84 (2 July)	MNR (Thomas)
1968	both species (14 July)		MNR (Thomas)
1973	both species (18 June)		Hogan (pers. obs.)
1974	both species (17 May)		Hogan (pers. obs.)
1975	both species (6 May)		Hogan (pers. obs.)
1976	157 (23 April-11 Sept)	370 (23 April-11 Sept)	Hogan (pers. obs.)
1977	158 (21 March-1 Sept)	369 (21 March-1 Sept)	Hogan (pers. obs.)
1978	150 (11 June)	403 (11 June)	Hogan (pers. obs.).

[a] Maritime Nest Records Scheme, Canadian Wildlife Service, Sackville, N.B.

Appendix V. Known histories of Prince Edward Island *P. carbo* colonies at East Point, McKinnon Point, Chepstow and High Bank. The dates of the nest counts (where available) are in parentheses.

Year	Nests (n)			
	East Point	McKinnon Point	Chepstow	High Bank
1935-1937	first seen	?	?	?
1946	30-40	15	?	?
1948	?	?	3 (20 June)[a]	?
1952	34 (3 June-13 July)	31+ (3 June-13 July)	?	?
1960	35 (13 July)	46 (13 July)	?	?
1963	57 (9 June)	45 (9 June)	?	?
1966	65 (5 June)	23+ (5 June)	?	?
1967	81+ (11 June)	?	?	?
1970	40-50+ (17 June)	?	?	?
1973	50+	15+	9	first report (no count)
1974	121 (29 June)	16+ (25 June)	?	211 (25 June)
1976	131 (5 July)	17+ (12 May)	26 (23 July)	236 *P. carbo* (16 July) 2 *P. auritus*
1977	119 (19 July)	54 (29 June)	36 (29 June)	241 *P. carbo* (19 June) 9 *P. auritus*
1978	?	40-45 (7 June)	49 (7 June)	216 *P. carbo* (4 June) 0 *P. auritus*

Note: 1935-1970 from Erskine (1972) and Maritime Nest Records Scheme

1973 from Brown *et al.* (1975)

1974-1978 Hogan (pers. obs.)

[a] reference to a colony by Godfrey (1954) in this vicinity may be Chepstow.

Appendix VI. Mean measurements (length x width in mm) of *P. carbo* eggs from 3-, 4-, 5- and 6-egg clutches at Durell Point in 1977.

Clutch-size	clutches (n)	Egg number					
		1	2	3	4	5	6
3	15	63.1 x 41.0	62.7 x 40.9	64.2 x 40.5	--	--	--
	S.E.	0.83 x 0.35	0.91 x 0.40	0.72 x 0.32	--	--	--
4	44	63.5 x 41.2	63.3 x 41.4	63.0 x 41.4	62.9 x 41.0	--	--
	S.E.	0.39 x 0.17	0.38 x 0.18	0.44 x 0.15	0.50 x 0.15	--	--
5	56	63.7 x 41.5	63.0 x 41.8	63.2 x 41.8	63.7 x 41.5	63.3 x 41.2	--
	S.E.	0.28 x 0.15	0.26 x 0.13	0.31 x 0.16	0.29 x 0.15	0.28 x 0.14	--
6	9	63.5 x 41.2	62.1 x 41.0	62.7 x 41.3	63.3 x 41.2	63.3 x 40.8	63.7 x 40.7
	S.E.	0.39 x 0.34	1.03 x 0.49	0.36 x 0.52	0.65 x 0.29	0.66 x 0.34	0.78 x 0.24

Appendix VII. Recoveries of *P. carbo* banded as nestlings at Durell Point between 1974 and 1977.

Band number	Date banded	Date recovered	Recovery location	Fate
628-79007	21 June 1974	6 October 1974	Tracadie, New Brunswick	found injured--died
628-79064	21 June 1974	2 November 1974	Salisbury, Massachusetts	found dead
638-71549	16 June 1975	hunting season 1975	near Ruffin, South Carolina	shot
638-71577	16 June 1975	20 October 1975	Gashouse Beach, Massachusetts	found dead
638-71509	16 June 1975	3 November 1975	South Bay, Lubec, Maine	found dead
638-71566	16 June 1975	December 1975	lower east Pubnico, Nova Scotia	shot
638-71568	16 June 1975	14 May 1977	2 mi. E Sydney Mines, Nova Scotia	entangled in fishing gear
638-69148	21 June 1976	19 October 1976	McNutts Island, Nova Scotia	entangled in fishing gear
638-69063	8 June 1976	24 October 1976	3 mi. W River John, Nova Scotia	found dead
668-71231	23 June 1977	3 October 1977	E. of Harpswell, Maine	found dead
668-71330	16 June 1977	18 October 1977	near North Cape, Prince Edward Island	entangled in fishing gear
668-71259	28 June 1977	9 December 1977	near St. George's Island, Maryland	trapped-dead
668-71346	16 June 1977	December 1977	Pasquotank River area, North Carolina	entangled in fishing gear
668-71248	23 June 1977	December 1977	Jones Harbour, Nova Scotia	shot
668-71306	12 June 1977	24 December 1977	Willard Beach, Maine	found dead
638-69170	5 June 1977	25 March 1978	Salem, Massachusetts	?
668-71371	19 June 1977	15 May 1978	Isle au Haut, Maine	found dead
628-79092[a]	23 June 1974	12 March 1975	near Stumpy Point, North Carolina	entangled in fishing gear

[a] *P. auritus* banded as a nestling at Cape Tryon.

Appendix VIII. Hatching and fledging success of *P. carbo* at Durell Point in 1977 analyzed according to various split dates of the clutch-start distribution.

Split dates	Nests (n)	Eggs Hatched/ Egg Laid	Chicks Fledged/ Egg Hatched	Chicks Fledged/ Egg Laid
12-27 April (pre-peak)	35	0.60	0.83	0.50
28 April-14 May (peak)	65	0.52	0.83	0.43
15 May-2 July (post-peak)	29	0.39	0.73	0.29
12 April-4 May[1]	69	0.58	0.83	0.48
5 May-2 July	60	0.45	0.78	0.35
12-23 April[2]	16	0.57	0.82	0.47
2-4 May	23	0.54	0.80	0.44
19 May-2 July	17	0.17	0.56	0.10
12-20 April[3]	12	0.57	0.91	0.52
21-29 April	26	0.64	0.81	0.52
30 April -8 May	51	0.52	0.82	0.43
9-17 May	18	0.49	0.76	0.37
18-26 May	13	0.36	0.83	0.30
27 May-2 July	9	0.16	0.00	0.00

[1] split date based upon a 50/50 split of the clutch-starts

[2] split dates based upon distinct early, middle and late samples of the clutch-starts

[3] split dates based upon continuous 9-day intervals throughout the breeding season

Appendix IX. Number of chicks fledged per nest for cormorant species from other studies.

Species	Chicks fledged per nest	Source
P. carbo sinensis	1.8	Kortland in Drent *et al.* 1964
P. aristotelis	1.3-2.3	Snow 1960
P. auritus	2.4	Drent *et al.* 1964
P. pelagicus	2.0	Drent *et al.* 1964
P. carbo carbo	1.2	Lock and Ross 1973
P. varius	0.83	Norman 1974